SILURIAN DALMANITACEAN TRILOBITES FROM NORTH AMERICA AND THE ORIGINS OF THE DALMANITINAE AND SYNPHORIINAE

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ABSTRACT. The dalmanitacean trilobite genera *Daytonia*, *Ommokris*, *Glyptambon*, and *Lygdozoon* are described from the Silurian of North America. *Daytonia* and *Ommokris* are assigned to the Dalmanitinae; *Glyptambon* belongs to the Dalmanitidae but cannot be referred to an established subfamily; and *Lygdozoon* is assigned to the Synphoriinae, together with the genus *Delops* Rickards, 1965. Synphoriinids have previously been reported only from strata of Early and Middle Devonian age. The predominantly Ordovician subfamily Mucronaspidinae is erected for some of the genera formerly included in the Dalmanitininae, and it is proposed that the Dalmanitinae and the genus *Glyptambon* arose from different members of the Mucronaspidinae, whereas the Synphoriinae had its origins in the Dalmanitininae.

TRILOBITES of the superfamily Dalmanitacea are abundant and diverse in the Silurian and Devonian of North America but have attracted little attention since the work of Delo (1935, 1940). Recent studies have concentrated on Devonian faunas (Lespérance and Bourque, 1971; Lespérance, 1975; Campbell, 1977) and consequently there is need for a revision of most previously described Silurian species. All of the species described here are assigned to new genera; they are of importance because they provide information on evolutionary relationships within the superfamily, in particular on the origins of the subfamilies Dalmanitinae and Synphoriinae. Most of the species are from the St. Clair Limestone (Wenlockian) of northern Arkansas, although some forms from other localities are also included. Other dalmanitacean species from the St. Clair are described by Holloway (1980).

Terminology in the descriptions largely follows Harrington, Moore and Stubblefield (*in* Moore, 1959) with the following additions. 'Eye socle' is used in the sense of Shaw and Ormiston (1964, p. 1002). Points of curvature on the facial suture are denoted by Greek letters, according to the scheme of R. and E. Richter (1949, p. 69). The term 'pseudo-articulating half ring' is applied to the depressed lenticular or subrectangular structures that are present on the front of some pygidial axial rings (apart from the first) where the posterior edge of the preceding ring has a medial embayment (Pl. 97, fig. 8, Pl. 102, fig. 1). These structures are separated from the ring proper by a transverse furrow. Symbols used in the synonymies are explained by Matthews (1973). Collection localities in the St. Clair Limestone referred to in the text are described by Holloway (1980).

SYSTEMATIC PALAEONTOLOGY

Order PHACOPIDA Salter, 1864
Suborder PHACOPINA Struve *in* Moore, 1959
Superfamily DALMANITACEA Vogdes, 1890
Family DALMANITIDAE Vogdes, 1890

Remarks. Kobayashi and Hamada (1971) erected the monotypic subfamily Langgoniinae within the Dalmanitidae for their new genus *Langgonia* from the Silurian of West Malaysia. Their descriptions and photographs show that *Langgonia* is characterized by an inflated, bulb-shaped glabella with a median longitudinal furrow on the frontal lobe and nodular lateral lobes; the presence of two nodular lobes overhanging the axial furrow on the posterior part of the fixigena (called 'paraglabellar

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lobes' by Kobayashi and Hamada); large holochroal eyes; an inflated pseudoglabellar region on the front of the librigena; functional connective sutures; and a pygidium with prominent, well-rounded (exsag.) pleural ribs that tend to merge behind the axis, deep pleural furrows, and no interpleural furrows (note that Kobayashi and Hamada refer to the pleural furrows as interpleural furrows). The presence of holochroal eyes and functional connective sutures would exclude *Langgonia* from the Dalmanitidae, and moreover from the suborder Phacopina, while the other features suggest that this genus should be referred to the Encrinuridae.

Subfamily DALMANITINAE Vogdes, 1890

1976 Perycopyginae Benedetto and Martel *in* Baldis *et al.*, p. 208.

Diagnosis. Cephalic apodeme 1p approximately equidistant from occipital and 2p apodemes; 1p and 2p apodemal pits more or less transverse and slit-like or comma shaped. Eyes large, extending close to posterior border furrow. Anterior and lateral cephalic border broad, flattened, meeting doublure at a sharp angle; except in some early forms, lateral border with shallow epiborder furrow extending backwards along genal spine. Posterior border furrow typically lanceolate in outline, generally not meeting lateral border furrow; genal spine flattened in cross section, steeply inclined laterally. Posterior border of hypostome elongate, with three denticles on rear edge. Thoracic pleural tips pointed, almost straight at front of thorax but progressively more posteriorly curved towards the back. Pleural furrows on thorax and pygidium typically long (exsag.), lanceolate in outline, generally deflected backwards distally behind articulating facet; anterior pleural bands slope steeply into pleural furrows, posterior bands (particularly on pygidium) slope more gently. Pygidium multisegmented, with well-defined border and mucro; pygidial apodemes transverse.

Remarks. Campbell (1977) has reviewed the Dalmanitinae and proposed new criteria for its definition. The preceding diagnosis is based on his work, with some modifications to accommodate early dalmanitinids such as *Daytonia* and *Prodontochile* Kobayashi and Hamada, 1971. None of the features mentioned by Benedetto and Martel (*in* Baldis *et al.*, 1976) in their diagnosis of the Perycopyginae distinguish this subfamily from the Dalmanitinae. In their discussion they list as particularly characteristic of their subfamily the subtriangular cephalon, the absence of an anterior cephalic process, the transglabellar 2p furrow, and the flat pygidium. A cephalic process is absent in many dalmanitids, including some species of *Dalmanites* and most species of *Odontochile*. The other features listed are either characteristic of dalmanitids in general or are of no more than specific importance. The illustrations of *Pericopyge* show no other characters justifying the separation of the genus from the dalmanitinids, and I consider it to be a synonym of *Dalmanites*.

Genus DAYTONIA n. gen.

Name. From Dayton, Ohio, near which the type species occurs. Gender feminine.

Type species. *Dalmanites Werthneri* Foerste, 1885 from the Brassfield Limestone (lower Upper Llandovery, C_1), Soldiers Home Quarries, near Dayton, Ohio.

Diagnosis. Anterior cephalic border subparallel-sided or with slight, well-rounded median process; lateral cephalic border weakly convex, epiborder furrow absent. Posterior border furrow meeting lateral border furrow distally; genal spine fairly short, slender and flattened, not longitudinally furrowed. Occipital ring strongly contracted behind the occipital apodeme; glabellar furrows 1p and 2p converging slightly abaxially, 1p with a distinct forward flexure proximally. Pleural furrows on thorax and pygidium short (exsag.), firmly impressed but tending to merge with pleural bands. Pleural furrows on anterior thoracic segments curve slightly forwards distally on to articulating facet; on posterior segments they are almost straight. Thoracic pleural tips pointed, progressively more strongly deflected backwards on posterior segments. Pygidium with about twelve axial rings and ten pleural furrows, a short mucro, and a broad, gently convex border. Posterior pleural bands approximately equal in height and length (exsag.) to anterior bands; interpleural furrows deeply impressed. Dorsal surface of exoskeleton granulate.

Remarks. The subfamilial assignment of *Daytonia* is problematical because this genus possesses some features that are characteristic of the Dalmanitinae, whereas others are more typical of the Mucronaspidinae. The features considered to be characteristic of the Dalmanitinae include (1) the presence of a 2p apodeme; (2) the long anterior cephalic border with a slight process medially; (3) the large eyes that extend back almost to the posterior border furrow; (4) the strongly asymmetrical profile (exsag.) of the pleural furrows on the thorax and pygidium; and (5) the form of the thoracic pleural tips. Features of *Daytonia* considered to be characteristic of the Mucronaspidinae are (1) the partial isolation of the 1p lobe by a short (exsag.) longitudinal furrow; (2) the abaxial convergence of the 1p and 2p furrows; (3) the shortened (exsag.) outer part of the occipital ring; (4) the gently convex lateral cephalic border, lacking an epiborder furrow; (5) the posterior border furrow that meets the lateral border furrow distally; (6) the thoracic pleural furrows that extend on to the articulating facets distally instead of running behind them; and (7) the posterior pleural bands on the pygidium that do not fade abaxially.

There are two other features of *Daytonia* that are worthy of note. The genal spines are flattened in section, as they are in dalmanitinids, but they are shorter and more slender, and are not longitudinally furrowed. The genal spines in Mucronaspidinae, on the other hand, are ovate in section. The pleural furrows on the thorax of *Daytonia* are not expanded (exsag.) as they are in most dalmanitinids, but the anterior and posterior pleural bands are depressed adjacent to the pleural furrows. These depressed regions are separated from the remainder of the pleural bands by a distinct change of slope, along which the exoskeletal granulation is interrupted (see Pl. 96, fig. 13). On the anterior pleural bands this change of slope runs into the pleural furrow proximally and distally, while on the posterior pleural bands it is subparallel to the pleural furrow. Pleural furrows of this form could have given rise to those of typical dalmanitinids by merging of the depressed portions of the pleural bands with the pleural furrows; (on internal moulds the pleural furrows of *Daytonia* seem to dominate the thoracic segments, as they do in normal dalmanitinids; Pl. 96, fig. 14). In the pygidium of *Daytonia* the pleural furrows seem to have already incorporated the depressed parts of the pleural bands, and the changes in slope referred to are visible only on the posterior bands of the first few segments.

Daytonia is thus transitional in morphology between the Mucronaspidinae and the Dalmanitinae, and is believed to represent an intermediate evolutionary stage (see discussion on the origin of the Dalmanitinae). In assigning the genus to the Dalmanitinae I have placed emphasis on the presence of a 2p apodeme, the form of the thoracic pleural tips, and the incipiently dalmanitinid form of the thoracic and pygidial pleural furrows.

Kobayashi and Hamada (1971) described a new dalmanitinid genus *Prodontochile* which they considered to be intermediate between the Zeliszkellinae (in the sense of Struve, *in* Moore, 1959) and the Dalmanitinae. The type and only known species, *P. igoi*, is from the Silurian of West Malaysia. *Prodontochile* shows some similarity to *Daytonia* in several features, such as the relatively narrow lateral cephalic border apparently lacking an epiborder furrow; the lack of a well-developed anterior cephalic process; the intersecting posterior and lateral cephalic border furrows; and the slender, unfurrowed genal spine. In its remaining features, including the glabellar segmentation, the lanceolate outline of the posterior border furrow on the cephalon, and the form of the thoracic pleural furrows (see Kobayashi and Hamada, 1971, pl. 20, fig. 7), *Prodontochile* is a normal member of the Dalmanitinae. Thus *Prodontochile* seems to be morphologically intermediate between *Daytonia* and *Dalmanites*, and could have been derived from a form similar to *D. werthneri*. Conodonts and graptolites occurring at the same horizons as *P. igoi* indicate that the age of the species is in the range early Late Llandovery (C_1) to early Wenlock (Igo and Koike, 1968, p. 4; Jones, 1968, p. 1269). It is thus of similar age to *D. werthneri*, or possibly somewhat younger.

Most of the features shared by *Daytonia* and *Prodontochile* are also found in the species *Phacops weaveri* Salter, 1849 from the latest Llandoverian (Telychian) of Great Britain (see Curtis, 1958, pl. 29, figs. 7–10). These features would exclude *P. weaveri* from the genus *Dalmanites*, to which it has generally been referred. *P. weaveri* differs from *Daytonia* mainly in that the anterior cephalic border is very short (sag., exsag.); the cheeks are relatively smaller, particularly in front of the eye; the occipital ring is not as contracted (exsag.) abaxially; and the 1p lobe is not partially isolated by a short longitudinal furrow.

Daytonia werthneri (Foerste, 1885)

Plate 96, figs. 1–9, 13, 14

v* 1885 *Dalmanites Werthneri* Foerste, pp. 116–117.
v. 1887 *Dalmanites Werthneri* Foerste; Foerste, p. 101, pl. 8, figs. 22, 22*a*, 23–25.
v. 1893 *Dalmanites Werthneri* Foerste; Foerste, pp. 530–1, pl. 27, figs. 22, 22*a*, 23–25 (not 1895 as stated by Weller, 1907, p. 197, and Delo, 1940, p. 52; figures copy of Foerste, 1887).
v. 1940 *Dalmanites werthneri* Foerste; Delo, p. 52, pl. 4, figs. 13, 14 (copy of Foerste, 1887, pl. 8, figs. 22, 23).

Type material. Lectotype (here designated): USNM 84799a, a complete dorsal exoskeleton with the anterior cephalic border broken; figured by Foerste (1887, pl. 8, fig. 24), but now prepared to reveal the pygidium; Pl. 96, figs. 13, 14. The paralectotypes include a number of cephala and an incomplete pygidium under the catalogue number USNM 84799. The locality given for these specimens was the Clinton Limestone at Soldiers Home Quarries, near Dayton, Ohio. In 1893 (p. 518) Foerste stated that the Clinton Group near Dayton is overlain by the Dayton Limestone, which indicates that the types of *D. werthneri* came from the unit now called the Brassfield Limestone.

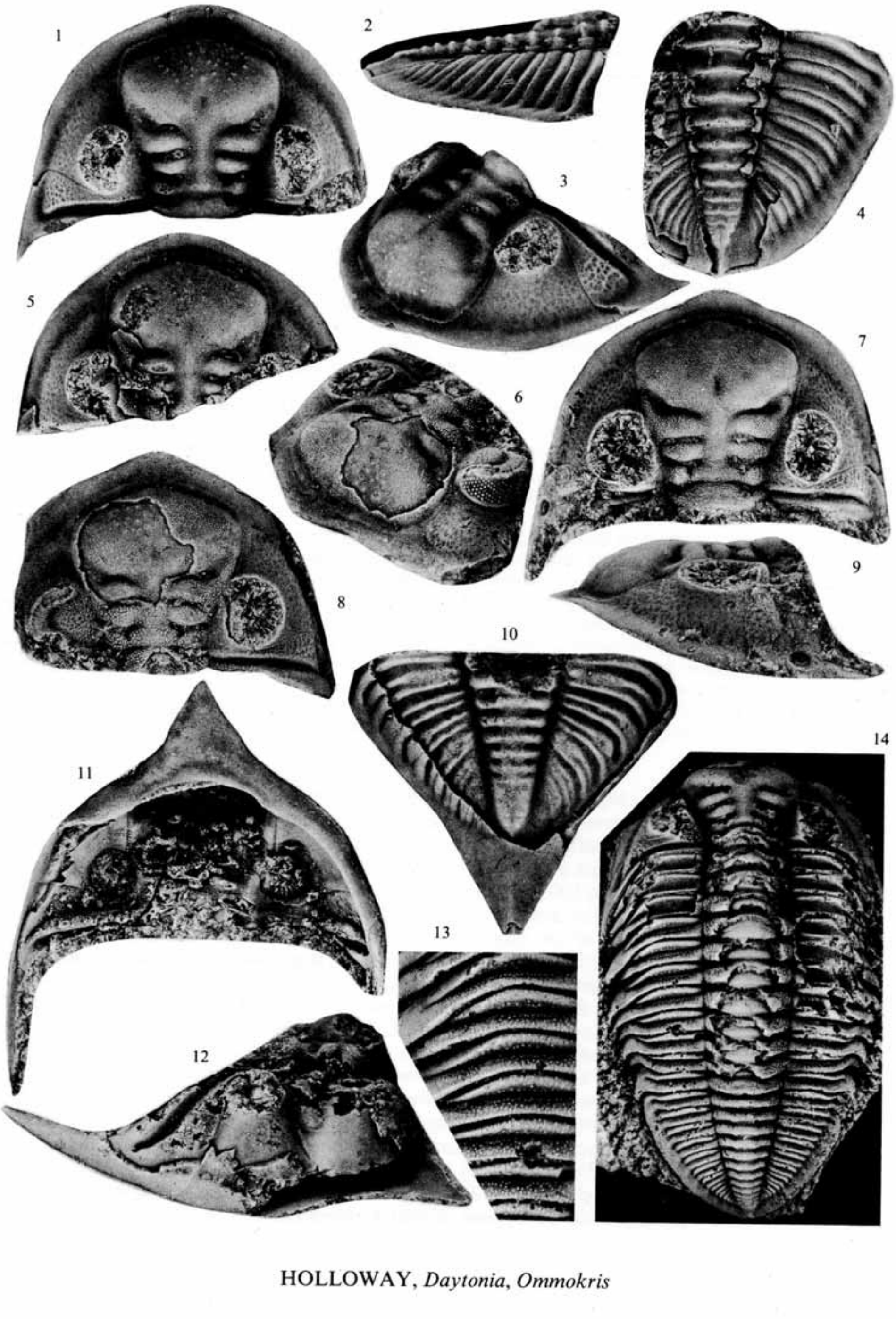
Description. Cephalon 1·75 times as wide across the genal spines as long (sag.); anterior outline with a distinct change in curvature directly in front of the eyes and a very slight, well-rounded median projection. Glabella equal in width at the occipital ring and 1p lobe, expanding gently from the 1p furrow to the front of the eye and even more gently thereafter; maximum width 1·58 times the minimum width. Axial furrow sharper in front of γ–γ than behind but fading adjacent to the frontal glabellar lobe; preglabellar furrow well defined. Occipital ring more strongly arched (tr.) than the remainder of the glabella, weakly turned forwards distally; occipital furrow bowed forwards slightly between the occipital apodemes. Inner ends of the glabellar furrows equally spaced and joined by a shallow longitudinal depression. 1p and 2p furrows meet the axial furrow distally; a short, rapidly diminishing furrow running backwards from the 1p furrow partially isolates nodular lateral 1p lobes. Inner section of the 3p furrow deep and transverse; outer section shallower, expanded and oblique, failing to meet the axial furrow. Frontal glabellar lobe comprises one half the length (sag.) of the glabella; in its posterior half is a median longitudinal furrow connected back to the inner ends of the 3p furrow by weak depressions (Pl. 96, fig. 7). Auxiliary impressions on the inner surface of the frontal lobe form a triangular pattern with the posterior apex at the median longitudinal depression.

EXPLANATION OF PLATE 96

Figs. 1–9, 13, 14. *Daytonia werthneri* (Foerste, 1885), Brassfield Limestone (Late Llandoverian), Soldiers Home Quarries, near Dayton, Ohio. 1, 3. Paralectotype, internal mould of cephalon USNM 84799f; dorsal and left oblique views, × 2·9. 2, 4. Paralectotype, pygidium USNM 84799b, figured by Foerste (1887, pl. 8, fig. 23); lateral and dorsal views, × 3·1. 5. Paralectotype, exfoliated cephalon USNM 84799e; dorsal view, × 3·6. 6, 8. Paralectotype, cephalon USNM 84799d; left oblique and dorsal views, × 3·3. 7, 9. Paralectotype, cephalon USNM 84799a, figured by Foerste (1887, pl. 8, fig. 22); dorsal and lateral views, × 3·1. 13, 14. Lectotype, almost complete dorsal exoskeleton USNM 84799c, figured by Foerste (1887, pl. 8, fig. 24); 13, enlargement of part of thorax showing form of pleural furrows, × 5·3; 14, dorsal view, × 2·8.

Figs. 10–12. *Ommokris bassleri* (Ulrich and Delo *in* Delo, 1940), St. Clair Limestone (Wenlockian), Locality USNM 286w, Batesville district, Arkansas. 10. Exfoliated pygidium PU 57674; dorsal view, × 2·2. 11, 12. Poorly preserved cephalon PU 88119 prepared to show the external mould of the doublure; 11, latex cast in ventral view, × 1·6; 12, right oblique view of specimen, × 1·6. Note that the oblique projection from the hypostomal suture in fig. 11 is caused by excessive excavation of matrix.

PLATE 96



HOLLOWAY, *Daytonia*, *Ommokris*

Eyes incompletely preserved but contain at least seven lenses per dorsoventral file near the midlength (exsag.); palpebral lobe gently convex (tr.) and with a narrow outer rim. Anterior branch of the facial suture initially runs parallel to the axial furrow, diverges gently from it at the anterolateral extremity of the frontal lobe, and gently converges with the preglabellar furrow medially. Posterior branch of the facial suture curves anterolaterally across the central part of the cheek and turns more strongly backwards across the border; ϵ and ω both level with the medial part of the occipital furrow. Lateral border widens slightly anteriorly, anterior border does not decrease in length appreciably in front of the glabella. Lateral border furrow broad, shallow and poorly defined, particularly anteriorly. Posterior border uniformly expanding abaxially, maximum convexity (exsag.) at the fulcrum. Posterior border furrow firmly impressed and becoming sharper abaxially, curving slightly backwards distally and shallowing.

Glabella thickly covered with 0·05–0·1 mm diameter granules which are sparser and weaker on the axial portions of lobes 1p, 2p, and 3p than on the lateral portions. Remainder of the cephalon bears slightly smaller granules of rather uniform density. Cheeks inside the border furrows (including the palpebral area but excluding the palpebral lobe) covered with shallow, poorly defined depressions up to 0·2 mm in diameter.

Thorax composed of eleven segments; axis increasing slightly in width (tr.) as far as the fifth segment and then narrowing just as gradually; pleurae curved steeply downwards at the fulcrum and (in posterior profile) reflexed outwards towards the tips. Front of the axial ring indented one third the way across by the apodeme; axial furrow notches the back of each segment but otherwise is shallow.

Pygidium 1·25 times as wide as long (sag.) and moderately convex (tr.), the border being separated from the remainder of the pleurae by a marked decrease in slope; lateral margins curve strongly inwards and gently upwards posteriorly. Axis almost as wide anteriorly as the pleurae, tapering evenly backwards and terminating with a rather pointed tip at the inner edge of the border, but connected to the mucro by a strong postaxial ridge. There are ten complete and two incomplete axial rings plus a terminal piece. All of the axial rings are strongly rounded (sag., exsag.) but the first stands much higher medially than the rest; a well-developed pseudo-articulating half ring is present on the medial part of the second ring and much smaller ones on rings three and four. Paired, subrectangular muscle impressions on the front of the axial rings on internal moulds are distinguishable almost to the axial termination (Pl. 96, fig. 4). There are ten pleural furrows which are successively more arcuate and posteriorly directed; they expand gently towards the fulcrum and then contract. Interpleural furrows short (exsag.) and sharply impressed but expand slightly distally. Anterior pleural bands have sharply rounded crests but posterior bands more flattened (exsag.) at the fulcrum and slope forwards. Articulating facet wide (tr.) and short (exsag.), its anterior margin gently embayed. Mucro broken off, but was clearly very small and triangular in cross-section proximally.

Axial rings on thorax and pygidium covered with coarse granules like those on the glabella. Finer granules on the pleurae decrease in abundance into the pleural furrows and near the axial furrow, but increase in density on the pygidial border.

Remarks. Foerste (1885, p. 116) stated that the eyes of *D. werthneri* contain thirty-five dorsoventral lens files with six or seven lenses each near the middle of the eye. In the syntypes that I have examined the eyes are too incomplete to confirm the number of dorsoventral files, but it is clear that there were at least seven lenses in the longest file. Foerste also stated that pygidia were very abundant in his material, but the syntypes in the USNM included only one pygidium, prior to the preparation of the lectotype. The pygidium of the lectotype does not have median tubercles on the axial rings, as described by Foerste; the axis of the other pygidium is exfoliated and so it is not possible to determine whether pustules were originally present. There is a discrepancy between the numbers of pygidial axial rings and pleurae given by Foerste (1885), who counted 13 axial rings and 10 pleurae, and Delo (1940), who stated that there are 9 or 10 rings and 6 or 7 pleurae. The correct number in the lectotype is 10 complete and 2 incomplete axial rings and 10 pleural furrows. Delo's description is also incorrect in stating that the cephalic borders are smooth; in fact they bear fine granules.

The species from the Jupiter Formation (Late Llandovery) of Anticosti Island figured by Bolton (1972, pl. 8, figs. 13, 24) as *Dalmanites jupiterensis* Twenhofel may be closely related to *D. werthneri.* It shows a close resemblance to species of *Eudolatites*, but the broad anterior cephalic border with a slight medial process, the large eyes, and the flattened genal spine suggest that it belongs to *Daytonia* rather than to the Mucronaspidinae. It is not possible to tell from the illustration whether a 2p apodeme is present. The species differs from *D. werthneri* in having a greater number of axial rings (fourteen complete and one incomplete) and pleural furrows (eleven) in the pygidium, shorter (exsag.) pygidial pleural furrows, and a relatively larger mucro. Published illustrations of the holotype of *Dalmanites jupiterensis* provide no information on relationships, but this specimen seems to differ from Bolton's specimen in having relatively larger eyes (see Twenhofel, 1928, pl. 60, fig. 3).

Genus OMMOKRIS n. gen.

Name. From the Greek 'omma' meaning eye and 'okris' meaning projection, referring to the very prominent eyes. Gender feminine.

Type species. Dalmanites bassleri Ulrich and Delo *in* Delo, 1940, from the St. Clair Limestone (Wenlockian), Batesville district, Arkansas.

Diagnosis. Anterior cephalic border contracted at base of frontal process, which is long, subtriangular or rod-like, and upwardly curved distally. Glabella as wide as long (sag., excluding occipital ring), expanding strongly between occipital furrow and anterior end of palpebral furrow and more weakly thereafter. Occipital ring decreases in length (exsag.) abaxially; 1p apodeme oblique, tending to be closer to occipital apodeme than to 2p apodeme; 2p apodeme subcircular or comma-shaped in plan. Cheek rising steeply from border furrows and becoming subvertical beneath eye; base of eye almost equal in height to glabella and markedly overhanging cheek. Eyes tall, turret-like and placed far back on cheek, anterior edge opposite inner end of 3p furrow and posterior edge overhanging posterior border furrow. Genal spine slender. Pygidium relatively small for a dalmanitinid; lateral margins straight, outline distinctly triangular. There are ten to sixteen axial rings and eight to ten pleural furrows; pleural furrows short (exsag.) for a dalmanitinid; interpleural furrows sharp and deep. Mucro flattened in cross-section proximally. Most of exoskeleton covered with fine granules.

Remarks. The cephalic apodemes of *Ommokris* show some similarity to the synphoriinid pattern, in that 1p is strongly oblique and often placed close to the occipital apodeme, and 2p is reduced in width (tr.) (see Pl. 97, fig. 4). However the cephalic borders and border furrows, the genal spines, and the pygidial architecture are all dalmanitinid in form so that there is no doubt about the subfamilial assignment of the genus.

Other species assigned to the new genus are *O. obex* n. sp. from the Niagaran dolomites of Illinois, *Dalmanites vigilans* Hall, 1861 from the Niagaran of Wisconsin, and *D. croneisi* Ball and Delo, 1940 from the Silurian of southeastern Missouri. Both *O. obex* and *O. vigilans* are of Wenlockian age; according to Ball and Delo, *O. croneisi* came from the Brassfield Limestone, which in southeastern Missouri is now referred to as the Sexton Creek Limestone, and is of Middle to Late Llandovery age (Berry and Boucot, 1970). However Ball and Delo noted that the horizon with *O. croneisi* contains faunas that are apparently younger than the type Brassfield, while a typical Brassfield fauna occurs stratigraphically lower in the sequence. Thus *O. croneisi* may be younger than Llandoverian.

Ommokris is distinguished from *Dalmanites* mainly by the long anterior cephalic process; the form of the cephalic apodemes; the highly elevated eyes situated far back on the cheeks; the relatively shorter (exsag.) pleural furrows on the pygidium (compare with *D. rutellum* Campbell, 1967, pl. 18, figs. 1-13); and the generally smaller number of pygidial axial rings and pleural furrows. Campbell (1977, p. 85) noted that in the form of the cephalic process and the contracted anterior cephalic border, *O. vigilans* shows certain similarities to his new subgenus *Huntonia* (*Huntonia*) from the Early Devonian of Oklahoma. Certain species of *H.* (*Huntonia*) also resemble *Ommokris* in the shape of the glabella and in the form of the cephalic apodemes (see Campbell, 1977, pl. 40, fig. 4*c*). *H.* (*Huntonia*) differs from *Ommokris*, however, in that the eyes are relatively longer (exsag.) and lower; the base of the anterior cephalic process is strongly convex on the ventral surface; the anterior cephalic border is more strongly contracted at the base of the process; there is a greater number of pygidial axial rings and pleural furrows, the pleural furrows are more expanded (exsag.), and the interpleural furrows are weaker; the pygidial axis does not extend as far back as the posterior few pleural ribs but is connected to the mucro by a strong postaxial ridge; the lateral pygidial margins are not straight but curve inwards towards the mucro; and the mucro is much narrower at the base and is upturned. In view of these differences, particularly in the form of the eyes, there seems to be little possibility of a close relationship between *Ommokris* and *Huntonia*, and so the suggestion by Campbell (1977, p. 85) that a new subgenus of *Huntonia* might be erected for Silurian species such as *O. vigilans* is not accepted. Certain Ludlovian species of *Dalmanites* such as *D. rutellum* Campbell, 1967, while not having a long anterior cephalic process, resemble *Huntonia* in the form of the glabellar and pygidial segmentation and in the shape of the mucro. These species are probably close to the ancestral stock of *Huntonia*. *Ommokris* apparently gave rise to no later forms, but seems to have been an early, terminating sidebranch from the main dalmanitinid evolutionary line.

Ommokris bassleri (Ulrich and Delo *in* Delo, 1940)

Plate 96, figs. 10–12; Plate 97, figs. 1–12

v. 1901 *Dalmanites* (*Synphoria*) *vigilans* Hall; Van Ingen, pp. 67–69 (in part; not *D. vigilans* Hall, 1861).

v. 1929 *Dalmanites cf. vigilans* Hall; Thomas, pp. 126–128, pl. 10, fig. 15 (not pl. 10, figs. 18, 19 = *D. howelli* Ulrich and Delo *in* Delo, 1940).

v.* 1940 *Dalmanites bassleri* Ulrich and Delo; Delo, p. 37, pl. 3, fig. 11 (not pl. 3, fig. 10 = *Dalmanites* sp. 1 of Holloway, 1980).

Type material. Holotype: USNM 79113a, almost complete pygidium figured by Delo (1940, pl. 3, fig. 11), and refigured here in Pl. 97, figs. 1, 2; from the St. Clair Limestone, Locality USNM 286w, Batesville district, Arkansas. Note that the type locality is St. Clair Springs and not Cason Mine as stated by Delo (1940, p. 37). The paratype of *bassleri* was referred to the species *Dalmanites* sp. 1 by Holloway (1980) and the reasons for this assignment are presented there.

Other material. Eleven cephala, a hypostome, and ten pygidia from the St. Clair Limestone at Localities USNM 286w, USNM 438, USNM 438c, D and B.

Diagnosis. Anterior cephalic process subtriangular in outline, strongly rounded distally. Eye composed of thirty-one dorsoventral lens files of up to eight lenses each; around base of eye is a relatively wide strip of exoskeleton devoid of lenses. Pygidium with 8–10 complete and 3 incomplete axial rings and 9 pleural furrows. Axis decreases in width and height more rapidly between first and sixth ring than behind sixth ring. Posterior pleural band on second segment expanded in length (exsag.) distally and interpleural furrow behind is deflected backwards; similar expanded regions commonly developed on posterior pleural bands of segments three and four, but situated successively closer to axial furrow. Proximal width of mucro greater than anterior width of axis, its sides gently convex in outline proximally; faint sagittal ridge extends backwards from axial termination and increases in strength posteriorly, so that mucro becomes triangular in cross section.

Description. Cephalon 1·5 times as wide across the genal spines as long (sag., including the anterior process); anterior outline with a distinct change in curvature lateral to an exsagittal line through δ (Pl. 97, figs. 6, 12). Glabella considerably wider at the occipital ring than the 1p lobe, width at the frontal lobe almost twice the minimum width. Axial furrow rises steeply between the occipital furrow and the anterior end of the palpebral furrow (where its is very weak), falls just as steeply to the outer end of the 3p furrow and then falls more gradually, finally dying out at the widest part of the frontal lobe. Preglabellar furrow barely distinguishable

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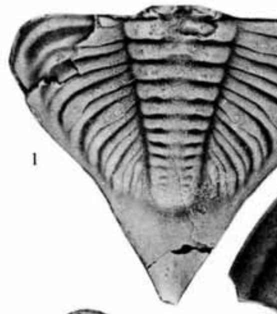
EXPLANATION OF PLATE 97

Figs. 1–12. *Ommokris bassleri* (Ulrich and Delo *in* Delo, 1940), St. Clair Limestone (Wenlockian), Batesville district, Arkansas. 1, 2. Plaster cast of holotype, pygidium USNM 79113a, figured by Delo (1940, pl. 3, fig. 11); dorsal and lateral views, ×2·0. Locality USNM 286w. 3. Poorly preserved hypostome USNM 256001; ventral view, ×2·4. Locality D. 4, 5. Incomplete cephalon PU 57656; dorsal and left oblique views, ×2·9. Note that the radial calcite prisms beneath the lenses of the right eye are diagenetic. Locality USNM 286w. 6. Incomplete cephalon USNM 255999; dorsal view, ×2·5. Locality D. 7. Incomplete pygidium USNM 256000; dorsal view, ×2·2. Locality USNM 438c. 8. Pygidium USNM 256002; dorsal view, ×2·9. 9, 11, 12. Latex cast of external mould of cephalon PU 88118; lateral, anterior, and dorsal views, ×2·0. Locality USNM 286w.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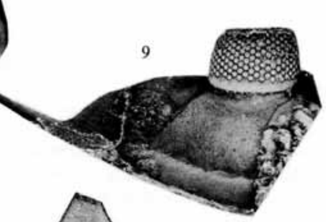
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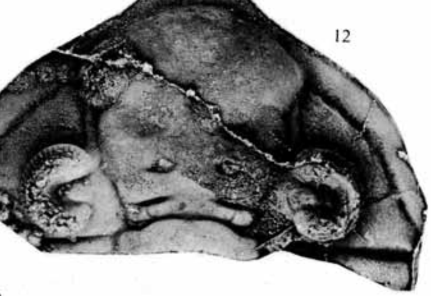
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11

HOLLOWAY, *Ommokris*

medially. Occipital ring more strongly arched (tr.) than the remainder of the glabella, gently concave abaxially in transverse profile, and with slight nodes distally; there is a weak median occipital tubercle. 2p and 3p lobes gently inflated, separated from axial part of glabella by a weak longitudinal furrow. Inner part of 3p furrow transverse, outer part expanded and oblique, in some specimens not reaching the axial furrow; a pattern of faint depressions radiates from the inner end of the 3p furrow (Pl. 97, fig. 6). Frontal lobe has a medial longitudinal pit just behind the midlength (sag.), and a pair of smaller, circular pits anterolaterally (Pl. 97, fig. 6).

Posterior border lower abaxially than the cheek in front; lateral to the fulcrum it is flexed downwards and backwards and stands higher than the cheek; posterior border furrow deepens laterally. Lateral border increases in slope posteriorly; a thin, raised rim on the border extends backwards along the lower edge of the genal spine (Pl. 96, fig. 12). Anterior border furrow shallow and poorly defined. Palpebral area rises very steeply from the axial furrow but is much lower than the palpebral lobe. Palpebral lobe divided into a narrow outer rim and a slightly higher, convex inner band by a line of coalesced pits; at its outermost point, palpebral furrow is tightly curved and expanded. In lateral profile, visual surface of equal height anteriorly and posteriorly but steeper posteriorly; lens arrangement in an almost complete eye is (commencing at the front): 4 5? 6? 7 7 7 8 7 8 8 7 8 7 8 7 8 7 8 7? 8? 7? 7? 6+ 6+ 6+ 6+ 5+ 5+ 4+ 4 2; lenses in the posterior file are very reduced in size, and a smaller accessory lens is present at the top of many files; a small granule is present on the sclera between three adjacent lenses. Between γ and β the anterior branch of the facial suture runs in a gentle furrow and is subparallel to the sagittal axis; thereafter it lies in the anterior border furrow abaxially and slightly behind it medially. Posterior branch of the suture runs in a sigmoidal arc to cross the lateral border furrow more or less opposite the middle (exsag.) of the eye, but is deflected sharply backwards half way across the border.

Anteromedial part of the doublure crossed by a weak, transverse depression running subparallel to the hypostomal suture; the latter is quite strongly convex forwards and at its distal ends the inner edge of the doublure has a marked change in curvature. Lateral part of the doublure narrows towards the genal spine. Posterior branch of the facial suture runs in a sigmoidal curve obliquely backwards across the doublure and cuts the inner edge just in front of the genal spine base.

Granules on dorsal surface of cephalon are slightly coarser on the medial part of the glabella, on the lateral and anterior borders, and on the basal part of the eye below the lowermost horizontal row of lenses; they are even coarser along the edges of the anterior cephalic process. Low, poorly defined swellings, also with superimposed granules, are scattered across the frontal glabellar lobe. Granules absent in the furrows (except the lateral border furrow), on the region of the cheek overhung by the base of the eye, and on the inner flange of the doublure. Between the granules on the lateral part of the doublure are linear pits.

A single specimen of a dalmanitinid hypostome was collected at Locality D in association with cephala and pygidia of *O. bassleri*. Lateral margins converge at a constant rate between the anterior wings and the shoulder, and at a greater rate behind the shoulder; obtuse posterolateral angles and the median angularity on the posterior margin probably originally bore spines. Middle body about as wide anteriorly as long (sag.), divided by a diagonal middle furrow ending in a deep pit in front of the weakly swollen macula. Anterior edge of the hypostome weakly upturned abaxially but a border not defined. Lateral border furrow straight and deep; lateral border narrow, expanding towards the shoulder from either direction. Posterior border furrow arcuate and shallowing medially; posterior border gently arched transversely. Surface of the hypostome badly weathered but granules distinguishable anteriorly and on the posterior border, and there are larger, weak swellings on the lateral part of the middle body.

Width of the pygidium across the articulating facets slightly exceeds the length (sag.); lateral margins converge at about 80° between the facet and the base of the mucro. In transverse profile axis is not evenly arched, the maximum curvature being sagittally; first eight or so axial rings defined by complete but medially shallowing ring furrows; thereafter axis divided by successively diminishing paired grooves that do not reach the axial furrow. Successively narrowing (tr.) apodemes are present on the first seven or eight segments, each apodeme with a flattened muscle insertion area on its anterior face; on internal moulds raised muscle scars are present on the more posterior segments, as far as the axial termination (Pl. 96, fig. 10). There is a deep, subrectangular embayment in the posterior edge of the first axial ring, and a smaller one on the second ring. Axial furrow shallowing posteriorly and not impressed behind the axis. Pleural furrows increase in length (exsag.) and in depth abaxially; anterior and posterior pleural bands flattened on top proximally and convex beyond the fulcrum. Doublure concave (tr.) beneath the mucro. Granules along the lateral margins of the pygidium and on the doublure are coarser than elsewhere.

Remarks. Authorship of this species is here attributed to Ulrich and Delo (*in* Delo, 1940) for the reasons given by Holloway (1980) in the discussion of *Dalmanites howelli*. *O. bassleri* is very close morphologically to *O. vigilans*. The types of *O. vigilans* include two cephala, both with the eyes broken off (Pl. 98, figs. 9, 12), but Hall (1867, pl. 21, fig. 17) figured another cephalon (apparently now lost) with the tall, turret-like eyes intact. *O. vigilans* is distinguished from *O. bassleri* by its relatively shorter anterior cephalic process, a greater number of axial rings and pleural furrows in the pygidium, and a mucro that is relatively narrower at the base.

O. croneisi is based only on pygidia (Pl. 98, figs. 1–3) but Ball and Delo (1940, pl. 1, fig. 10) figured a fragmentary cephalon occurring with the type specimens and which they considered possibly to belong to the same species. This seems likely, since they described it as having 'highly elevated' eyes. I am unable to detect any significant differences between the pygidia of *O. croneisi* and those of *O. bassleri*, and the cephalon referred to above shows insufficient features to distinguish it. Ball and Delo (1940, p. 405) stated that *croneisi* 'appears to be identical with an undescribed species which occurs in the St. Clair Limestone of Arkansas', but in later erecting *bassleri*, Delo (1940) made no reference to *croneisi*, which suggests that he may have reversed this opinion. Discovery of additional material of *croneisi* may prove it to be a senior synonym of *bassleri*, in which case it would become type species of *Ommokris*, unless a case could be made for its suppression. This problem could have been avoided by nominating either *O. vigilans* or *O. obex* as type species, but these are represented by relatively few specimens that are poorly preserved and do not show all of the diagnostic characters of the genus, and their localities are imprecisely known.

Van Ingen (1901, pp. 67–69) referred 'large numbers of fragmentary cephala and pygidia' from the St. Clair Limestone at St. Clair Springs to *Dalmanites* (*Synphoria*) *vigilans*, but did not figure any of the specimens. Of this material, eight cephala and a pygidium can be recognized amongst the Van Ingen collections at Princeton University. Most of these belong to *O. bassleri*, but one of the cephala belongs to *Dalmanites howelli* Ulrich and Delo, and another to a species of *Dalmanites* described by Holloway (1980) as *Dalmanites* sp. 2. The presence of more than one species accounts for the dimorphism reported by Van Ingen. Van Ingen also stated that specimens from Wisconsin and Indiana referred to *D. vigilans* by Hall (1867, 1877) exhibited dimorphism. He considered cephala from Wisconsin and pygidia from Indiana to belong to one dimorph, while cephala from Indiana and pygidia from Wisconsin belonged to another. The Indiana specimens are now assigned to a separate species, *D. halli* Weller, 1907.

Ommokris obex n. sp.

Plate 98, figs. 6, 10, 11, 13, 16

v. 1907 *Dalmanites vigilans* Hall; Weller, pp. 276–278, pl. 24, figs. 1–4 (*non D. vigilans* Hall, 1861, p. 51).
v. 1940 *Dalmanites vigilans* Hall; Delo, pp. 51–52, pl. 3, figs. 3–5.

Name. Latin 'obex' meaning bar, referring to the form of the anterior cephalic process.

Type material. Holotype: UC 9879, an internal mould of a cephalon encrusted with dolomite crystals; Pl. 98, figs. 10, 11, 16. Paratype: UC 10747, internal mould of pygidium; Pl. 98, figs. 6, 13. Both from Niagaran dolomites near Lemont, Illinois.

Diagnosis. Anterior cephalic process subcylindrical and rod-like, strongly upturned, ventral surface flattened proximally. Pygidium wider than long (sag.); mucro short, narrower proximally than anterior width of axis. There are 9 or possibly 10 axial rings and 7 or possibly 8 pleural furrows; axis weakly arched (tr.); pleurae slope weakly outwards adaxially and are strongly downturned distally.

Remarks. The types of *O. obex* were figured by Weller (1907, pl. 24, figs. 1, 2, 4) and Delo (1940, pl. 3, figs. 3–5) as *Dalmanites vigilans*. *O. obex* is distinguished from other species of *Ommokris*, including *O. vigilans*, by the form of the anterior cephalic process. It differs from *O. bassleri* additionally in that the posterior branch of the facial suture does not curve as strongly forwards across the cheek, so that it crosses the lateral border furrow well behind the middle (exsag.) of the eye; the pygidium is relatively wider and has fewer axial rings and pleural furrows; the pygidial axis is not as convex (tr.); and the mucro is relatively smaller.

Subfamily DALMANITININAE Destombes, 1972

Diagnosis. Apodeme 1p wide (tr.), directed obliquely backwards from axial furrow and slightly expanded proximally; 2p apodeme not developed. Occipital ring decreases in length (exsag.) abaxially behind occipital apodeme; nodular 1p lobes commonly defined by weak furrow joining inner ends of occipital and 1p apodemes. Eyes generally small, posterior edge lying distant from posterior border furrow. Anterior and lateral cephalic borders rather narrow, rolled downwards along outer edge; in dorsal view anterior border almost non-existent medially; posterior border furrow sharply impressed, meeting shallow lateral border furrow distally; genal spines (if present) slender, circular in cross section. Lateral part of cephalic doublure narrow, strongly rounded; anterior part with distinct swelling medially. Hypostome subquadrate or subrectangular, lacking shoulders; middle body divided by shallow middle furrow into subparallel-sided anterior lobe and short (sag.) posterior lobe. Pleural bands on thorax and pygidium well-rounded (exsag.); pleural furrows thick and deep. Towards front of thorax, pleurae strongly facetted and extremities bear a deep notch and a short, rounded posterior process; segments towards back of thorax more weakly facetted and tips obliquely truncated; pleural furrows curve forwards across articulating facets on all thoracic segments. Pleural furrows on pygidium almost straight, interpleural furrows shallow and sharply impressed; anteriormost pleural furrow terminates against posterior edge of articulating facet. Pygidial doublure narrow and strongly rounded.

Genera assigned. *Dalmanitina* Reed, 1905; *Crozonaspis* Henry, 1968.

Remarks. The concept of this subfamily put forward by Destombes (1972) is modified here by the removal of some genera to the new subfamily Mucronaspidinae. In addition, some of the features included by Destombes in his diagnosis, such as the relative depths of the glabellar furrows and the number of pygidial axial rings and pleurae are not considered to be of importance in distinguishing the subfamily. The Dalmanitininae and Mucronaspidinae are very closely related, as shown by the similarities in the glabellar furrows and cephalic apodemes, the form of the cephalic borders and doublure, and the hypostome. However, these features, amongst others, distinguish both subfamilies from the Dalmanitinae. The Dalmanitininae differ from the Mucronaspidinae mainly in the progression in shape of the pleural tips from notched at the front of the thorax to obliquely truncated further back; the pleural furrows that curve forwards across the articulating facets on all of the

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EXPLANATION OF PLATE 98

Figs. 1–3. *Ommokris croneisi* (Ball and Delo, 1940), Brassfield Formation (Llandoverian), Little Saline Creek, St. Genevieve County, Missouri. 1. Plaster cast of paratype, incomplete and exfoliated pygidium UC 34689; dorsal view, ×2·5. 2, 3. Plaster cast of holotype, internal mould of pygidium UC 34689A, figured by Ball and Delo (1940, fig. 11); lateral and dorsal views, ×2·5.

Figs. 4, 7. *Glyptambon verrucosus* (Hall, 1864), St. Clair Limestone (Wenlockian), Locality USNM 286vi, Batesville district, Arkansas. Cephalon USNM 256004; lateral and dorsal views, ×1·5.

Figs. 5, 8, 9, 12, 15. *Ommokris vigilans* (Hall, 1861), Niagaran dolomites, Waukesha, Wisconsin. 5. Syntype, pygidium AMNH 39275; dorsal view, ×2·0. 8. Syntype, internal mould of pygidium AMNH 39274; dorsal view, ×2·0. 9. Syntype, internal mould of cephalon AMNH 39276; dorsal view, ×2·0. 12, 15. Syntype, internal mould of cephalon AMNH 39273, figured by Hall (1867, pl. 21, fig. 16); dorsal and lateral views, ×2·0.

Figs. 6, 10, 11, 13, 16. *Ommokris obex* n. sp., Niagaran dolomites near Lemont, Illinois. 6, 13. Plaster cast of paratype, internal mould of pygidium UC 10747, figured by Weller (1907, pl. 24, fig. 4) as *Dalmanites vigilans* Hall, 1861; lateral and dorsal views, ×2·4. 10, 11, 16. Holotype, incomplete internal mould of cephalon UC 9879, figured by Weller (1907, pl. 24, figs. 1, 2) and Delo (1940, pl. 3, figs. 3, 4) as *Dalmanites vigilans* Hall, 1861; 10, 16, lateral and dorsal views, ×2·3; 11, ventral surface of anterior process, ×3·8.

Fig. 14. *Lygdozoon arkansanum* (Van Ingen, 1901), St. Clair Limestone (Wenlockian), Locality USNM 286w, Batesville district, Arkansas. Paralectotype, very small cephalon PU 57738; dorsal view, ×6·9.


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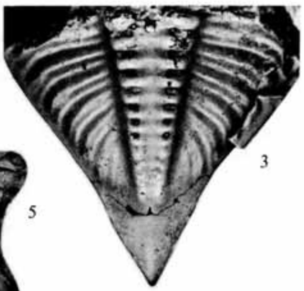
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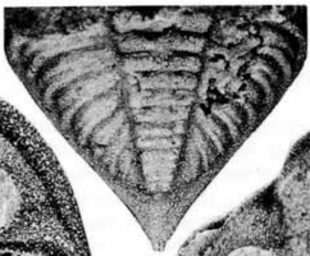
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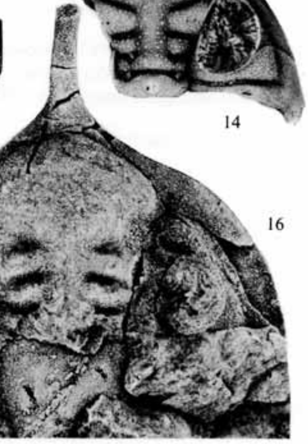
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HOLLOWAY, *Dalmanitacean trilobites*

segments; the well-rounded (exsag.) pleural bands on the thorax and pygidium; and the relatively long (exsag.) pygidial pleural furrows and shallow interpleural furrows that are not flexed strongly backwards distally (Pl. 100, figs. 8, 9).

When *Dalmanitina* enrolled the notches in the tips of the anterior thoracic segments aligned to form a continuous groove into which fitted the lateral cephalic doublure, while the posterior processes on the segments overlapped the margin of the cephalon. This is very well shown in the partially enrolled specimen figured by Destombes (1972, pl. 6, fig. 3). The oblique tips on the last few segments simply abutted against the anterior part of the cephalic doublure. In *Crozonaspis* the process on the anterior segments (Henry, 1968*b*, pl. 2, fig. 9) fitted into the vincular furrow in the lateral part of the cephalic doublure, if a vincular furrow was present (Clarkson and Henry, 1973, fig. 6B); otherwise closure must have been achieved in the same manner as in *Dalmanitina*.

Duftonia Dean, 1959 was transferred from the Acastinae to the Dalmanitininae by Ingham (1977). This genus has a pygidium that is similar in form to that of *Dalmanitina*, although the axis has a well-defined terminus instead of merging with the mucro. However the cephalic apodemes are narrower (tr.), stouter structures than those of the Dalmanitininae and Mucronaspidinae and the glabella is differently shaped, being relatively narrower across the 1p lobes and expanding more strongly in front of the 1p furrow. Furthermore Dean (1959, p. 147) stated that the thoracic pleural tips are all bluntly rounded, although this cannot be verified from his plates. The shape of the glabella and the form of the glabellar furrows, the very small, nodular 1p lobes, and the form of the thoracic pleural tips suggest to me that the affinities of *Duftonia* may lie with the Pterygometopidae. This supports the views of Whittington (1962, p. 12) who suggested a relationship between *Duftonia* and *Calyptaulax*.

Subfamily MUCRONASPIDINAE n. subfam.

Diagnosis. Cephalon and hypostome similar to those of Dalmanitininae. Pleural bands on thorax and pygidium not strongly rounded (exsag.), posterior band tends to slope more weakly into pleural furrow than anterior band. Pleural tips on anterior thoracic segments obliquely truncated, with rear edge extended into short, flattened spine; on more posterior segments pleural tips turned progressively more strongly backwards and spines increase in length. Articulating facets relatively small and subtriangular on all thoracic segments except first, which has a larger facet; on anterior segments pleural furrow runs on to the facet, on posterior segments not extending beyond the inner edge of facet. Pleural and interpleural furrows on pygidium sharply impressed, of similar strength, deflected strongly backwards abaxially; anteriormost pleural furrow not reaching inner edge of articulating facet. Pygidial doublure broad.

Genera and subgenera assigned. Mucronaspis Destombes, 1963; *Eodalmanitina* Henry, 1965; *Eudolatites* (*Eudolatites*) Delo, 1935; *E.* (*Banilatites*) Destombes, 1972; *E.* (*Deloites*) Destombes, 1972; *Retamaspis* Hammann, 1974; *?Chattiaspis* Struve, 1958.

Remarks. The specimens of *Mucronaspis* and *Eodalmanitina* figured by Destombes (1972, pl. 9, figs. 5, 8*a*, *b*) and Hammann (1974, pl. 5, figs. 82*a*, *b*) respectively, show well the obliquely truncated thoracic pleural tips with their rear edge drawn out into a spine; the pleural furrows that do not run on to the facets on the posterior thoracic segments; the posterior pleural bands on the thorax that slope more weakly into the pleural furrows than the anterior bands; and the short (exsag.), sharply incised pygidial pleural and interpleural furrows that are strongly flexed backwards distally.

The Mucronaspidinae resemble the Zeliszkellinae in the form of the glabellar furrows and cephalic apodemes, the convexity of the pleural bands, the relationship of the thoracic pleural furrows to the articulating facets, the backwardly deflected spines on the tips of the posterior thoracic segments, the sharpness of the pleural and interpleural furrows on the pygidium and the curvature of the interpleural furrows, and the broad pygidial doublure (Henry, 1968*a*, pls. A, B). Zeliszkellinids differ, however, in having relatively wider and more flattened anterior and lateral cephalic borders and doublure, a shallow vincular furrow on the lateral part of the doublure, a differently shaped hypostome, anterior thoracic segments with rounded tips and broad articulating facets, and pleural furrows on the pygidium that are almost straight.

Eodalmanitina was regarded as a synonym of *Mucronaspis* by Destombes (1972) and Hammann (1974). However on comparing the type species of each, *E. macrophthalma* is seen to differ from *M. termieri* in having a medially pointed anterior cephalic outline, a weakly forwardly expanding glabella, 2p furrows that are reduced in width (tr.) and often almost pit like, and flattened palpebral lobes that are not appreciably elevated above the palpebral area. Species with these features, such as *E. destombesi* (Henry), *E. destombesi nava* (Hammann) and *E. alnifensis* (Destombes) range from the latest Llanvirn to the early Caradoc. The *M. termieri* type is represented by species such as *M. danai* (Meek and Worthen), *M. mucronata* (Brongniart), *M. darraweitensis* (Campbell), *M. greti* (Destombes) and *M. zagoraensis* Destombes, all of which occur in the middle Caradoc–Llandovery interval.

Certain species of *Eodalmanitina*, such as *E. chillonensis* (Hammann, 1974, pl. 2, figs. 22–27), have pygidia that are unusual for members of the *Mucronaspis* group in having somewhat longer (exsag.) pleural furrows that are not distinctly turned backwards distally, and in lacking a border. However, in these species the articulating facet is not as oblique and its relationship to the first pleural furrow is the same as in the other representatives. *Retamaspis* Hammann, 1972 is closely related to these species of *Eodalmanitina*, differing only in the lack of genal spines and a pygidial mucro and in having fewer pygidial segments. It therefore seems to be better placed in the Mucronaspidinae rather than in the Zeliszkellinae as proposed by Hammann (1974).

Chattiaspis Struve, 1958 is tentatively included in the Mucronaspidinae because the pygidal pleural and interpleural furrows curve backwards distally in at least some of the specimens figured by Struve (1958, pl. 4). However, confirmation of this assignment must await further information on the structure of the thoracic pleurae. All that is known at present is that the posterior edge of each pleural tip is extended into a long spine (Henry and Nion, 1970, fig. 4).

Subfamily UNCERTAIN

Genus GLYPTAMBON n. gen.

Name. Greek 'glypter' meaning chisel and 'ambon' meaning border, referring to the shape of the anterior cephalic process. Gender masculine.

Type species. *Dalmania verrucosa* Hall, 1864 from the Waldron Shale (Wenlockian), Waldron, Indiana.

Diagnosis. Glabella fairly strongly convex for a dalmanitid, expanding forwards at almost constant rate; frontal glabellar lobe with distinct forward bulge medially. Cephalic apodemes transverse, almost equally spaced. Cheeks inside borders moderately inflated, crossed by broad, shallow furrows containing anterior and posterior branches of facial suture. Anterior cephalic process short (sag.), broad, and downturned, with transverse outline medially; anterior border contracted in front of lateral part of frontal glabellar lobe. Lateral border with shallow epiborder furrow extending on to genal spine; posterior border furrow not expanding appreciably abaxially, meeting lateral border furrow distally. Lateral part of cephalic doublure with shallow, poorly defined furrow that dies out anteriorly; anteromedial part of doublure with crescentic, depressed region behind anterior cephalic process. Thoracic pleurae broadly facetted, drawn out into fine, backwardly deflected spines distally. Pleural furrows short (exsag.) and sharp, curving laterally beyond the fulcrum and running on to articulating facets. Pygidium with eleven to thirteen axial rings and ten to eleven pleural furrows. Axis not terminating at inner edge of border but extending relatively undiminished in height to base of mucro; all except most posterior rings bear successively smaller pseudo-articulating half rings. Pleural and interpleural furrows on pygidium thin and bent strongly backwards distally; pleural furrows only slightly deeper than interpleural furrows. Anterior pleural bands weaker than posterior bands distally and successively reduced on more posterior segments until they disappear entirely. Mucro upturned. Pygidial doublure narrow, gently convex and inclined, with low flange along inside. Sculpture on dorsal exoskeleton of tubercles with superimposed and intervening granules; short, backwardly deflected medial spine present near posterior edge of occipital ring.

Remarks. The subfamilial position of *Glyptambon* is at present uncertain. A relationship to the Dalmanitinae is suggested by features such as the form and spacing of the cephalic apodemes, the relatively wide cephalic borders with an epiborder furrow, and the flattened genal spine with an extension of the epiborder furrow along its length. However there are certain other features in which *Glyptambon* differs from typical dalmanitinids. These differences are mainly in the thoracic and pygidial architecture and are as follows.

1. The posterior border furrow on the cephalon is not lanceolate in outline and it meets the lateral border furrow distally.

2. All of the thoracic pleurae curve strongly backwards distally and terminate in long, sharp spines.

3. The pleural furrows on the thorax and pygidium are not expanded in length (exsag.) but tend to be thin and sharply impressed. On the thoracic segments the pleural furrows run on to the articulating facets distally.

4. On the pygidium it is the anterior pleural bands, rather than the posterior, that fade abaxially, while the posterior bands are expanded and inflated distally so that on the last few segments they leave no room for the anterior bands.

5. The pygidial axis does not have a well-defined terminus but merges posteriorly with the mucro. This feature was also described by Lespérance (1975, p. 92); just how much importance can be attached to it is at present unclear.

The features listed above would exclude *Glyptambon* from the Dalmanitinae as the latter is diagnosed here, and I can see no way in which the diagnosis may be modified to take account of the new genus, without destroying the concept of the subfamily. I know of no other Silurian dalmanitacean, with the possible exception of *Struveria*, that may be related to *Glyptambon*. *Struveria* has a pygidium with a similar pleural rib structure, but there is no other evidence of a close relationship. It will probably be necessary to erect a new subfamily to receive *Glyptambon*, but until more is known about its relationships to other Silurian and Devonian dalmanitaceans, I prefer not to propose any formal taxonomic unit.

Note that most of the cephalic, thoracic and pygidial structures listed above represent a serial repetition of the same feature, being related to the form of the pleural furrow and the relative strengths of the anterior and posterior pleural bands on individual segments. They must therefore reflect a basic difference in organization between *Glyptambon* and members of the Dalmanitinae.

Glyptambon verrucosus (Hall, 1864)

Plate 98, figs. 4, 7; Plate 99, figs. 1–14; Plate 100, figs. 1–6; text-fig. 1.

*1864 *Dalmania verrucosa* Hall; pp. 218–220.
. 1877 *Dalmania verrucosa* Hall; Hall, pl. 33, figs. 5–17, pl. 34, figs. 13–15.
. 1879 *Dalmanites verrucosus* (Hall); Hall, pp. 195–196, pl. 33, figs. 5–17, pl. 34, figs. 13–15 (copy Hall, 1877).
. 1882 *Dalmanites verrucosus* (Hall); Hall, pp. 341–342, pl. 35, figs. 5–17, pl. 36, figs. 13–15 (copy Hall, 1877).
? 1907 *Dalmanites verrucosus* (Hall); Weller, pp. 280–281, pl. 25 figs. 6, 7.
. 1940 *Dalmanites verrucosus* (Hall); Delo, p. 51, pl. 4, figs. 3–5.

Type material. Lectotype (here designated): AMNH 36646, crushed dorsal exoskeleton with incomplete pygidium, figured by Hall (1877, pl. 33, fig. 7); refigured here in Pl. 99, fig. 14. Paralectotypes: AMNH 36644, small cephalon (Hall, 1877, pl. 33, fig. 5); AMNH 36645, small cephalon (Hall, 1877, pl. 33, fig. 6); AMNH 36647, cephalon (Hall, 1877, pl. 33, fig. 8); AMNH 36648, cephalon (Hall, 1877, pl. 33, fig. 9); AMNH 36649, cephalon (Hall, 1877, pl. 33, figs. 10, 11?); AMNH 36650, thoracic segment (Hall, 1877, pl. 33, fig. 12); AMNH 36651, small pygidium (Hall, 1877, pl. 33, fig. 13); AMNH 36652, small pygidium (Hall, 1877, pl. 33, fig. 14); AMNH 36653, pygidium (Hall, 1877, pl. 33, figs. 15, 16); AMNH 36654, pygidium (Hall, 1877, pl. 33, fig. 17); AMNH 36655, ventral surface of cephalon (Hall, 1877, pl. 34, fig. 13). The fragmentary pygidium figured by Hall (1877, pl. 34, figs. 14, 15) is apparently lost. All of the types are from the Waldron Shale at Conn's Creek, Waldron, Indiana (Hall, 1879, p. 99).

Other material. From the Waldron Shale: a complete dorsal exoskeleton. From the St. Clair Limestone, Locality USNM 286vi Batesville district, Arkansas: two cephala and four pygidia.

Description. Glabella equal in width at the occipital ring and 1p lobe; width at the frontal lobe almost twice the occipital width and equal to the length (sag., excluding the occipital ring). Occipital ring flattened medially in front of the spine and sloping steeply forwards to the occipital furrow; abaxially it increases in convexity and decreases slightly in length (exsag.). Posterior edge of occipital ring gently concave medially. 1p apodeme turned slightly forwards proximally and joined to the axial furrow distally by a 1p furrow; 2p apodeme slightly oblique, not joined to the axial furrow. 3p furrow quite deeply impressed. Axial furrow weakest adjacent to the posterior half of the 3p lobe; narrow and gently impressed elsewhere, including around the front of the glabella.

Anterior branch of the facial suture diverges gently from γ, curves forwards towards the lateral extremity of the frontal glabellar lobe, and thereafter runs subparallel to the preglabellar furrow. Posterior branch of the suture crosses the cheek in a sigmoidal curve, cutting the outer part of the lateral border more obliquely, so that ω is exactly opposite ϵ. Eye forms slightly more than a semicircle in plan, upper margin of much smaller radius of curvature than the lower. Visual surface high in profile, inclined at 25° to the vertical anteriorly, decreasing to 15° posteriorly. Lenses arranged in thirty-three to thirty-six dorsoventral files with a maximum of nine or ten lenses per file; typical lens formula is 3 5 6 7 8 8 9 9 9 9 9 9 9 9 9 9 9 10 9 9 9 9 8 9 9 8 8 8 8 8 7 7 6 5 2. Palpebral lobe rises fairly steeply from the palpebral furrow to slightly exceed the height of the glabella; narrow rim around the outside of the lobe is slightly lower than the crest inside. Posterior border almost as long (exsag.) proximally as the abaxial length of the occipital ring, tapers weakly towards the fulcrum and thereafter gradually expands. Lateral border gently inclined, epiborder furrow fades anteriorly and along the genal spine; lateral border furrow broad and gently impressed, shallowing posteriorly. Hypostomal suture gently concave; at its distal end the inner edge of the doublure has only a weak change in curvature. Crescentic depression on the medial part of the doublure runs obliquely off the inner edge at the distal end of the hypostomal suture.

Surface of glabella and cheeks (excluding the borders) covered with large, rounded tubercles with superimposed and interspersed granules; tubercles densest on the anteriorly sloping part of the frontal glabellar lobe; sparse and subdued on the palpebral area and inner part of the fixigena; absent in furrows, including the sutural furrows. Cheeks inside the borders bear weak pits between the tubercles. Cephalic borders and outer part of the doublure covered with closely spaced granules; there are a few scattered tubercles across the back of the posterior border. Inner surface of the genal spine and the doublure flange smooth.

Thorax composed of eleven segments. Axial rings similar in form to the occipital ring except that they increase in length (exsag.) abaxially; articulating furrow with a well-rounded base medially, deepening abaxially into anterolaterally directed apodemal pits. Axial furrow strongly notches the back of each segment, otherwise shallow. Pleural furrows sharply incised against the back of the anterior pleural bands but merging more gradually with the posterior pleural bands, thinning distally as they run on to the facet. Anterior pleural bands increase in length (exsag.) and convexity abaxially, posterior bands decrease in length and convexity as far as the fulcrum and then increase.

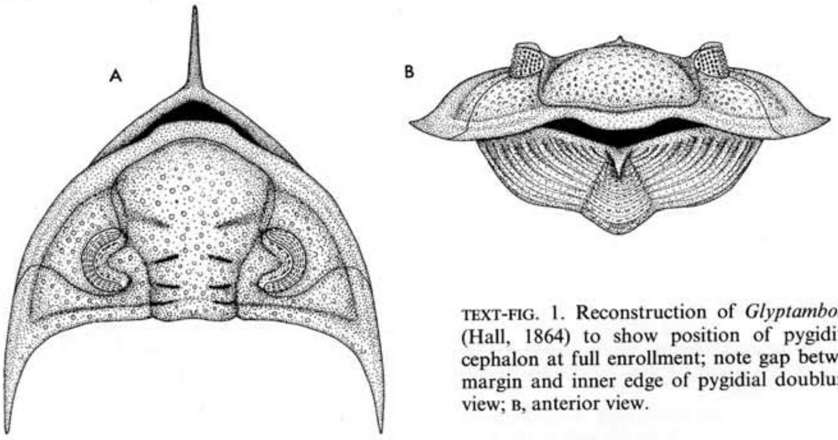
Pygidium 1·5 times as wide as long (sag., excluding mucro); lateral margins almost straight but curving gently inwards and upwards posteriorly to the base of the mucro. Axis changes in transverse profile from the front, where it is gently concave on the flanks, to the back, where it is evenly arched (Pl. 99, fig. 11). There are 11–13 axial rings, all except the very reduced (sag.) posterior ones being flattened (sag., exsag.) and sloping forwards in lateral profile; axial rings not defined on the posteriormost part of the axis that merges with the mucro. Ring furrows shallow medially, posterior ones being incomplete. Axial furrow weakens adjacent to the unsegmented portion of the axis.

Pleural and interpleural furrows of similar depth and with abrupt anterior slopes and more gentle posterior slopes; anteriormost pleural furrow runs behind the articulating facet distally. Expanded and elevated distal ends of the posterior pleural bands extend beyond the anterior bands on to the poorly defined border; ten pleural segments (and possibly a faint eleventh) distinguishable by the inflated ends of the posterior bands. Short (exsag.) articulating flange on the anterior pleural margin extends beyond the fulcrum and terminates at an obtuse process on the anterolateral corner of the articulating facet (Pl. 99, figs. 8, 9). Pygidia from the Waldron Shale have spike-like mucros that are almost half the length of the axis, flattened on their ventral surfaces proximally, and circular in cross-section distally; St. Clair pygidia have mucros that are tiny, upturned, thorn-like points.

Axial rings on the thorax and pygidium each have a transverse row of seven conical, backwardly deflected tubercles near the posterior edge; medial tubercle largest and most prominent, outermost one smallest and placed further forwards than the others. Interspersed with these tubercles are smaller tubercles, generally with no regular arrangement, although a median pair is consistently present on the first few axial rings of the pygidium, lying level with the front of the median tubercle. Anterior and posterior pleural bands bear transverse rows of tubercles that are smaller than those on the rings. Granules superimposed on and interspersed with tubercles on the axis and pleurae, but absent or rare along the front of the axial rings and pleural bands. On the pygidium, granulation is finer and denser towards the outer margin and on the doublure.

Remarks. The presence of a median occipital spine cannot be confirmed in the St. Clair material because the occipital ring is either incomplete or extensively weathered. Some of the Waldron specimens have suffered compression, resulting in a decrease in convexity and an increase in the width to length ratios of cephala and pygidia; this is particularly so for some pygidia. However, relatively undistorted specimens are similar in convexity and proportions to those from the St. Clair. The only significant difference between the Waldron and St. Clair specimens is in the length of the mucro. Mucro length is known to be very variable in dalmanitinid species however (see, for example, Campbell, 1967, pl. 16), and this difference is accounted for by geographic variation within a single species.

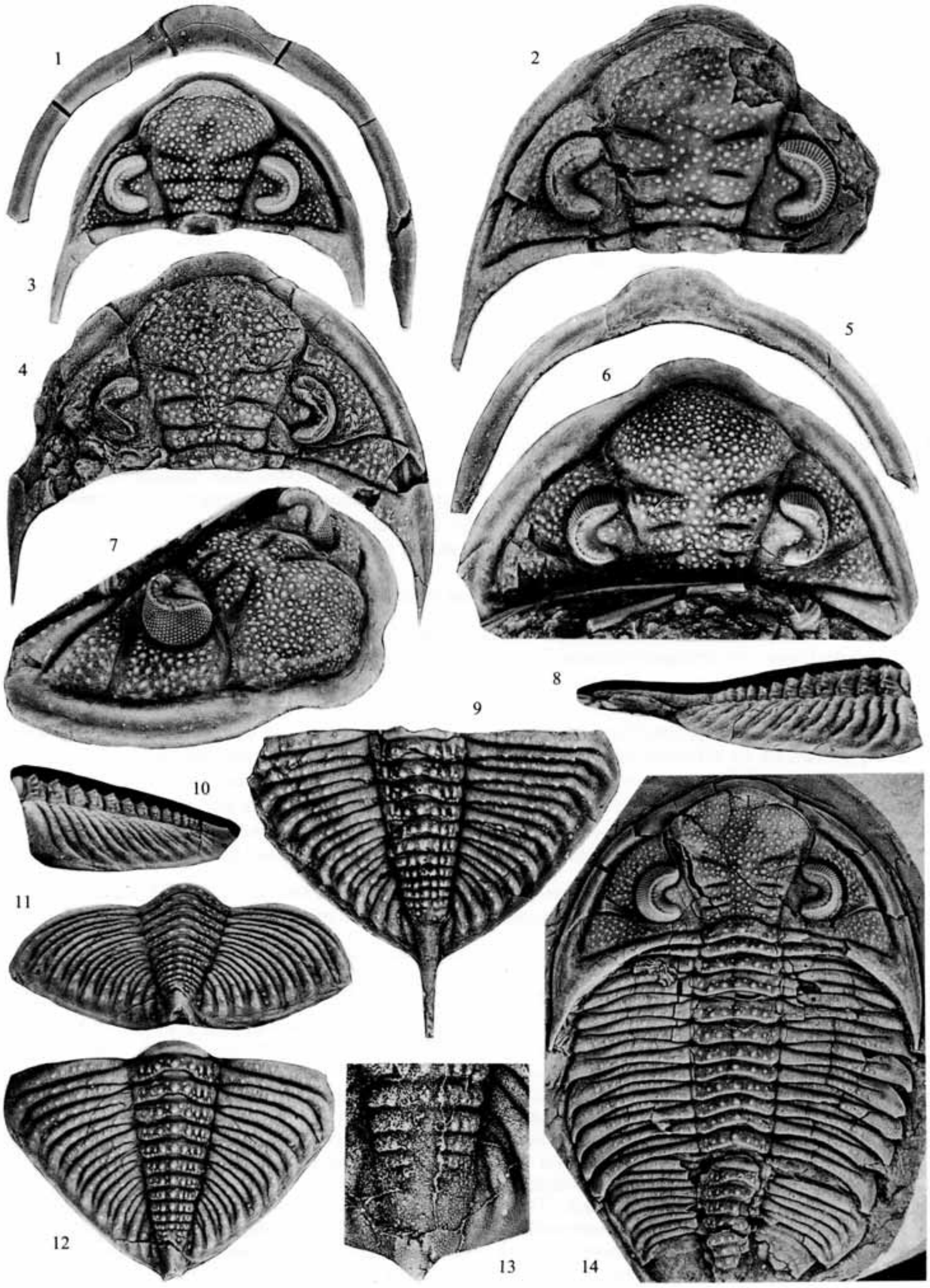
In dalmanitaceans the surfaces of the cephalic and pygidial doublures that meet during enrollment are relatively flat and come into contact over much of their extent, at least posteriorly. Thus even in the absence of articulated specimens it is possible to infer the relative positions of the cephalon and pygidium during enrollment from their outlines and from the maximum width of the pygidium in



TEXT-FIG. 1. Reconstruction of *Glyptambon verrucosus* (Hall, 1864) to show position of pygidium beneath cephalon at full enrollment; note gap between cephalic margin and inner edge of pygidial doublure. A, dorsal view; B, anterior view.

EXPLANATION OF PLATE 99

Figs. 1–14. *Glyptambon verrucosus* (Hall, 1864). All except fig. 13 from Waldron Shale (Wenlockian), Conn's Creek, Waldron, Indiana. 1. Paralectotype, doublure of incomplete cephalon AMNH 36655, figured by Hall (1877, pl. 34, fig. 13); ventral view, × 1·8. 2. Paralectotype, incomplete cephalon AMNH 36649, figured by Hall (1877, pl. 33, figs. 10, 11?); dorsal view, × 1·4. 3. Paralectotype, small cephalon AMNH 36644, figured by Hall (1877, pl. 33, fig. 5); dorsal view, × 3·1. 4. Paralectotype, cephalon AMNH 36647, figured by Hall (1877, pl. 33, fig. 8); dorsal view, × 1·0. 5–7. Paralectotype, cephalon AMNH 36648, figured by Hall (1877, pl. 33, fig. 9); ventral, dorsal and right oblique views, × 1·3. 8, 9. Paralectotype, pygidium AMNH 36654, figured by Hall (1877, pl. 33, fig. 17); lateral and dorsal views, × 1·3. 10–12. Paralectotype, pygidium AMNH 36653, figured by Hall (1877, pl. 33, figs. 15, 16); lateral, posterodorsal and dorsal views, × 1·3. 13. Latex cast of counterpart external mould of pygidium USNM 256006, showing granules on exoskeleton and tiny mucro (complete); dorsal view, × 4·0. St. Clair Limestone (Wenlockian). Locality USNM 286vi, Batesville district, Arkansas. 14. Lectotype, crushed dorsal exoskeleton AMNH 36646, figured by Hall (1877, pl. 33, fig. 7); dorsal view, × 1·1.



HOLLOWAY, *Glyptambon*

comparison with the width of the cephalon. This has been done by Campbell (1977) for the Early Devonian dalmanitaceans *Huntonia* (*Huntonia*), *H.* (*Prosocephalus*), and *Phalangocephalus*. In the case of *Glyptambon verrucosus*, it is clear that the posterior end of the pygidium must have projected a considerable distance in front of the cephalon, so that there would have been a gap between the inner edge of the pygidial doublure and the anterior cephalic border (text-fig. 1). Because the pygidial margin is deflected upwards posteriorly, and the cephalic border curves upwards towards the anterior process, there would also have been a slit between the edges of the cephalon and pygidium in anterior view. Campbell (1977) has interpreted similar gaps in *H.* (*Huntonia*), *H.* (*Prosocephalus*), and *Phalangocephalus* as allowing circulation of oxygen-bearing water to the exites, and in some forms they may also have allowed the protrusion of the antennae. Campbell suggested that when the antennae were fully withdrawn in *Huntonia* they lay crossed over in a shallow, arcuate furrow on the median part of the doublure immediately in front of the hypostomal suture. This offers an explanation for the crescentic depression on the medial part of the cephalic doublure in *Glyptambon*.

Family SYNPHORIIDAE Delo, 1935

Remarks. The concept of the Synphoriidae put forward by Lespérance (1975) has been substantially modified by Campbell (1977). Whilst retaining the subdivision into the Synphoriinae and the Trypaulitinae, Campbell has proposed new criteria for the recognition of these subfamilies, removed *Roncellia* from the Synphoriinae and *Forillonaria* from the Trypaulitinae, and reassigned both genera to the Dalmanitinae. He rejected the view that the principal diagnostic feature of the synphoriids is the distal coalescence of glabellar lobes 2p and 3p. Such coalescence is widespread throughout the Dalmanitacea and cannot be used to distinguish taxa of family or subfamily rank.

Subfamily SYNPHORIINAE Delo, 1935

Diagnosis. Distance between cephalic apodemes 1p and 2p more than 1·5 times that between occipital and 1p apodemes; 1p apodeme oblique; 2p reduced in width (tr.), tending to be subcircular in plan. Lateral cephalic border and doublure relatively narrow; border flattened dorsally but rolled downwards and inwards along outer margin. Genal spines (when present) slender, ovate in cross section, lacking a longitudinal furrow. Pleural furrows on thorax and pygidium deep, steep-sided, tending to run on to articulating facet distally; anterior and posterior pleural bands well-rounded (exsag.), of equal strength on pygidium. Pleural tips on thoracic segments rounded, except in early representatives in which they are rounded or pointed at front of thorax and towards the back are orthogonally truncated in a gentle curve or are deflected backwards into a spine. Pygidium lacking a well-defined border; apodemes on axial rings equidimensional in plan and isolated from axial furrow.

Remarks. The preceding diagnosis has been adapted from Campbell's (1977) analysis of the Synphoriinae so as to include *Lygdozoon* and *Delops* and some other slight modifications. Campbell

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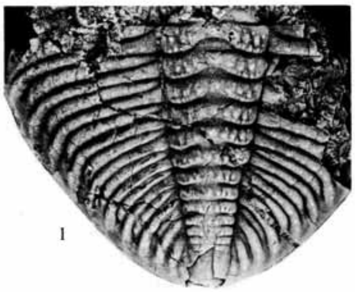
EXPLANATION OF PLATE 100

Figs. 1–6. *Glyptambon verrucosus* (Hall, 1864), St. Clair Limestone (Wenlockian), Locality USNM 286vi, Batesville district, Arkansas. 1, 2. Pygidium USNM 256006; dorsal and lateral views, × 1·6. 3–6. Incomplete cephalon USNM 256005; lateral, right oblique, ventral and dorsal views, × 1·7.

Figs. 7, 10. *Delops nobilis nobilis* (Thomas, 1900), Wenlock Shales near Builth, Powys, Wales. Holotype, figured by Thomas (1900, pl. 34, fig. 1) and Rickards (1965, pl. 85, figs. 7, 10). 7, latex cast of external mould OUM C25, dorsolateral view, × 1·3; 10, internal mould of same specimen OUM C24, dorsal view, × 1·3. Note the progressive change from pointed pleural tips on the anteriormost thoracic segments to spinose and backwardly curved tips on the more posterior segments.

Figs. 8, 9. *Dalmanitina socialis* (Barrande, 1846), Letná Formation (Caradocian), Veselá, Czechoslovakia. Internal mould of laterally compressed exoskeleton RSM 1856.30.456; 8, enlargement of thoracic pleurae in left lateral view, × 4; 9, right dorsolateral view, × 1·5. Note that all except the posterior few thoracic segments have notches in the pleural tips, into which the cephalic doublure fitted on enrollment.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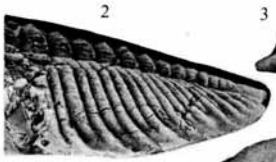
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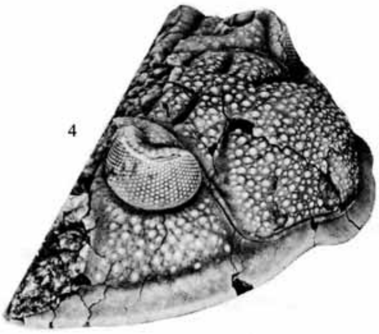
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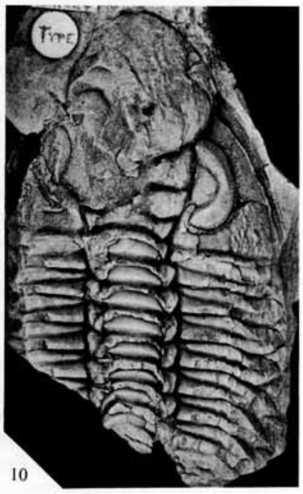

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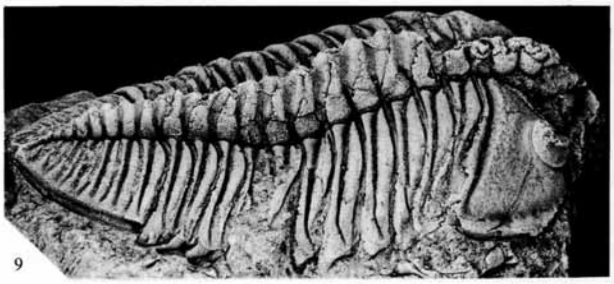
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HOLLOWAY, *Dalmanitacean trilobites*

(1977) stated that the lateral cephalic border in synphoriinids is narrow, convex, and poorly defined. However, the lateral border in the cephalon of *Synphoria sopita* figured by Lespérance (1975, pl. 1, fig. 10) is not evenly rolled but is flat-topped, and is separated from the rest of the cheek by a very weak border furrow. *Anchiopsis* appears to have a similar border, to judge from the poorly preserved internal mould figured by Lespérance and Bourque (1971, pl. 27, fig. 1). The essential difference between this type of border and that of dalmanitinids is that the former is relatively narrower and curves downwards and inwards along the outer edge, instead of meeting the doublure at a sharp angle.

Lygdozoon has many features reminiscent of Devonian synphoriinids and is believed to be ancestral to them. This was anticipated by Campbell (1977, p. 67) who suggested that the species *Dalmanites* (*Synphoria*) *arkansanus* Van Ingen, 1901, which is here included in *Lygdozoon*, may be close to the parent stock of the Synphoriinae. Similarities with Devonian synphoriinids include the spacing of the cephalic apodemes, the form of the lateral cephalic border and doublure, the construction of the genal spines, the well-rounded pleural bands on the thorax and the nature of the pleural furrows, and the over-all form of the pygidium, including the apodemes. The main differences are the 2p apodemes that are not as reduced in width (tr.), the lack of an anterior cephalic process and an eye socle, the relatively deeper lateral border furrows, and the shape of some of the thoracic pleural tips. With the exception of the thoracic pleural tips, these differences are minor or would not be unexpected in a primitive synphoriinid. Nothing can be said about the hypostome since hypostomes of Devonian synphoriinids are so poorly known.

Two types of thoracic segments belonging to the type species of *Lygdozoon*, *L. collatum*, have been found in the St. Clair Limestone. One type has a broad articulating facet and a strongly rounded pleural tip, as in Devonian synphoriinids, whereas the other type has a narrow facet and a truncated tip. In most dalmanitaceans the more anterior thoracic segments undergo more movement during enrollment than the posterior ones and hence are more strongly facetted. This can be seen in the specimen of *Dalmanites rutellum* figured by Campbell (1967, pl. 17, figs. 10, 12), and also in the holotype of *Delops nobilis nobilis* (Pl. 100, figs. 7, 10). This suggests that the round-tipped segments in *Lygdozoon* are from the anterior part of the thorax and that the segments with truncated tips are from the posterior part. The presence of truncated pleural tips on the posterior thoracic segments seems at first to be difficult to explain in a synphoriinid, but it is shown later that these are of phylogenetic significance.

Delops shares most features with *Lygdozoon* and seems to be very closely related. It differs from *Lygdozoon* mainly in the greater forward projection of the glabella relative to the lateral border, the shapes of the thoracic pleural tips, and the tuberculate surface sculpture. The shape of the genal spines is not known with certainty since in the specimens figured by Rickards (1965) they have either been flattened by compression or completely broken off. From the nature of the lateral cephalic border, however, they are more likely to have been ovate in section than blade-like as in dalmanitinids. The thoracic pleural tips are certainly unusual for a synphoriinid, being pointed on the anterior segments and becoming progressively more spinose and backwardly deflected towards the back of the thorax (Pl. 100, figs. 7, 10). However, this pattern could have been produced from the pattern in *Lygdozoon* by a decrease in the degree of rounding of the tips on the anterior segments and elongation of the tips on the posterior segments. It is possible that the differences in the pleural tips can be explained in terms of enrollment styles. Because the glabella and also the anterior border in *Delops* project so far forward with respect to the lateral border, the tips of the posterior thoracic segments may have extended outside the lateral border when the enrolled pygidium was in place beneath the median part of the cephalic doublure. Spinose tips may have been developed on these segments so as to extend up over the edge of the border. This hypothesis has not been checked, however, because the specimens of *Delops* that I have examined have no structures on the cephalic doublure to indicate the enrolled position of the pygidium.

Note that the cephalic apodemes in small holaspids of *Lygdozoon* and *Delops* do not have the synphoriinid spacing (Pl. 98, fig. 14; Pl. 103, fig. 14; Rickards, 1965, pl. 85, figs. 8, 9), but this is also true in *Synphoria* (Lespérance and Bourque, 1971, pl. 26, fig. 10).

Genus LYGDOZOON n. gen.

Name. Greek 'lygdos' meaning white marble, and 'zoon' meaning animal, referring to the occurrence of the type species in the St. Clair Limestone. Gender neuter.

Type species. *Lygdozoon collatum* n. sp. from the St. Clair Limestone (Wenlockian), Batesville district, Arkansas.

Diagnosis. Anterior cephalic border short (sag.), not modified by spines or crenulations; lateral border with faint epiborder furrow, lateral border furrow distinct. Genal angle rounded, pointed, or extended into slender spine. 1p apodeme more or less transverse, 2p generally oblique, not equidimensional in plan. Eye socle absent. Cephalic doublure without vincular furrow or only faintly furrowed laterally. Anterior thoracic segments with broadly facetted pleurae having sharply rounded tips; posterior segments more weakly facetted and orthogonally truncated distally in a gentle curve. Pygidium non-mucronate, with poorly defined axial terminus and well-rounded (tr.), rapidly diminishing postaxial ridge. Surface sculpture granular.

Remarks. Van Ingen (1901, pp. 69–73) described two distinct types of *Lygdozoon* cephala from the St. Clair Limestone, differing mainly in the presence or absence of genal spines. He referred both forms to his species *Dalmanites* (*Synphoria*) *arkansanus* and attributed the differences to sexual dimorphism. Examination of Van Ingen's material shows that there are in fact three types of cephala and two types of pygidia present, but although the specimens were all collected at St. Clair Springs, the type locality for the St. Clair Limestone, there is no indication that they were actually found together in the one horizon. In none of the later collections from the St. Clair are spined and unspined forms of *Lygdozoon* found to be associated. For example, forms without genal spines have not been recorded at Searcy Spring although more than one hundred cephala of *L. collatum* with genal spines have been collected from this locality. This evidence does not support Van Ingen's hypothesis of dimorphism, and accordingly forms of *Lygdozoon* with genal spines are here considered to belong to different species from those without genal spines.

The cephalon described as *Dalmanites arkansanus* by Weller (1907, pl. 24, fig. 5) from the Niagaran of Illinois (probably the Racine Dolomite) belongs to *Lygdozoon*, and I have also seen specimens of this genus from the Clarita Formation of south central Oklahoma, the Osgood Formation at Osgood, Indiana, and the Starcke Limestone of Texas. The age of these formations suggested by Berry and Boucot (1970) indicates a maximum range for *Lygdozoon* of Late Llandoverian to Ludlovian.

Lygdozoon collatum n. gen., n. sp.

Plate 101, figs. 1–17; Plate 102, figs. 1–13; text-fig. 2

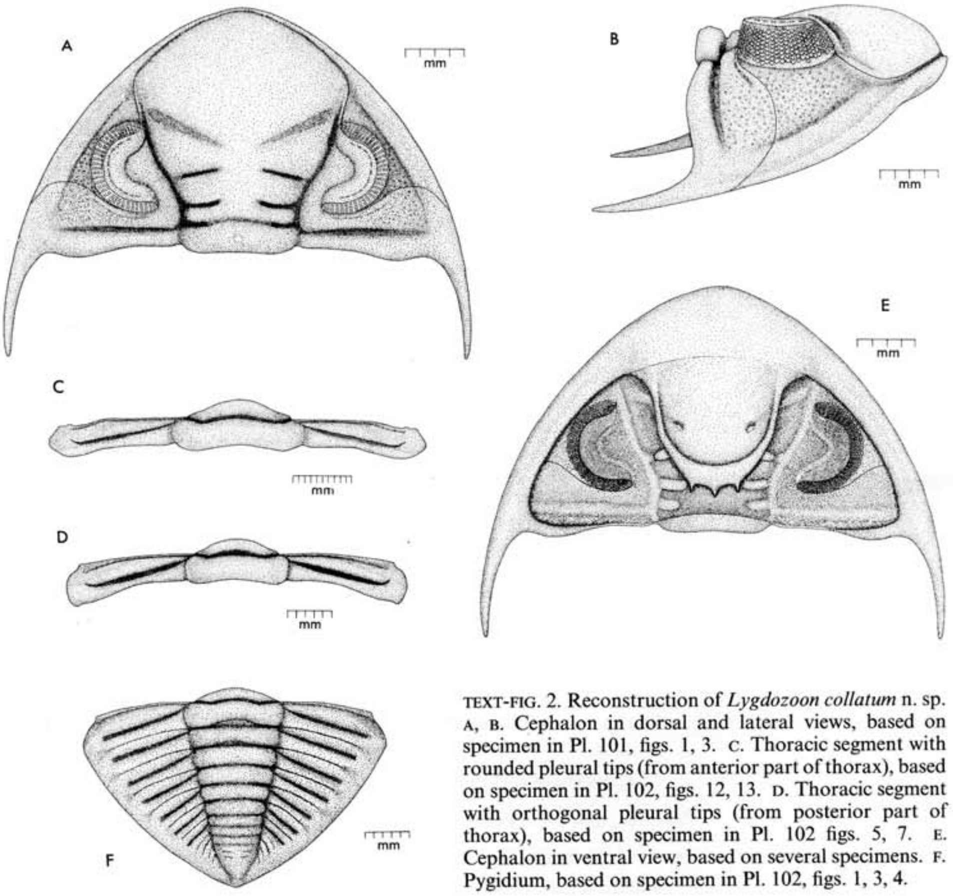
. 1929 *Dalmanites arkansana* Van Ingen; Thomas, pp. 125–126, pl. 10, figs. 12–14.

Name. Latin 'collatus' meaning gathered together or collected, referring to the abundance of this species in the St. Clair Limestone.

Type material. All from the St. Clair Limestone, Batesville district, Arkansas. Holotype; USNM 256007, incomplete cephalon; Pl. 101, figs. 1, 3, 10; from Locality USNM 438c. Paratypes. From Locality USNM 483c: USNM 298946, cephalon; USNM 298951, hypostome; USNM 298941, thoracic segment; USNM 298945, 298950, pygidia. From Locality USNM 286v: USNM 256008, 256011, 298949, cephala; USNM 298940, pygidium. From Locality H: USNM 256010, 298948, cephala; USNM 298947, hypostome; USNM 298937-8, 298942-3, thoracic segments. From Locality E: USNM 298944, pygidium. From an unknown locality: USNM 256012, pygidium.

Other material. There are abundant additional specimens of this species in the U.S. National Museum of Natural History, mainly from Localities USNM 438c and 286v.

Diagnosis. Species of *Lygdozoon* with genal spines, glabellar furrow 2p weakly joining axial furrow, and large eyes lying closer to sagittal axis posteriorly than anteriorly. Eye with 35 or 36 dorsoventral lens files of up to 9 lenses each. Pygidium with 10–11 axial rings (last 2 or 3 defined by incomplete ring furrows) and 9 pleural furrows.

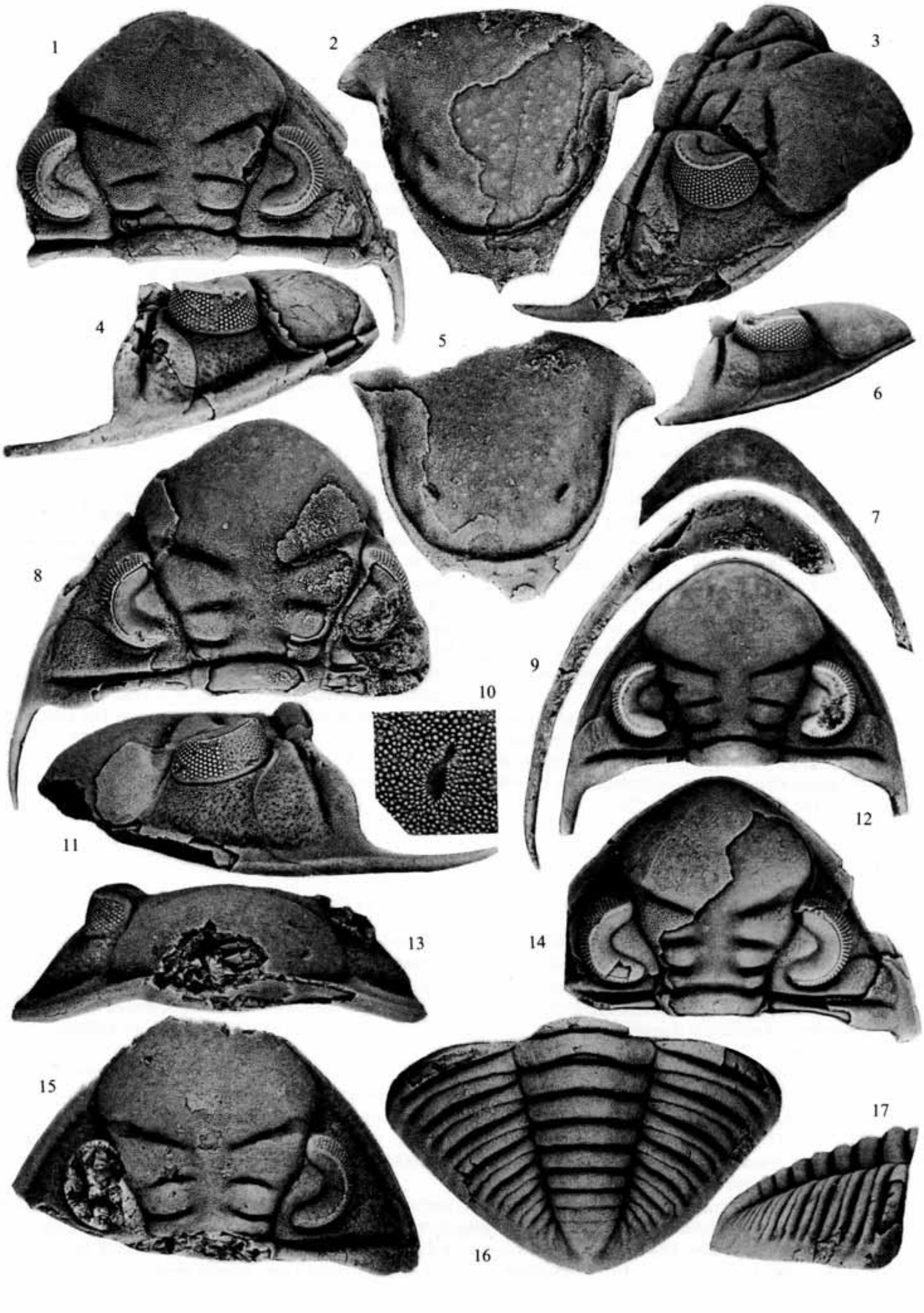


TEXT-FIG. 2. Reconstruction of *Lygdozoon collatum* n. sp. A, B. Cephalon in dorsal and lateral views, based on specimen in Pl. 101, figs. 1, 3. C. Thoracic segment with rounded pleural tips (from anterior part of thorax), based on specimen in Pl. 102, figs. 12, 13. D. Thoracic segment with orthogonal pleural tips (from posterior part of thorax), based on specimen in Pl. 102 figs. 5, 7. E. Cephalon in ventral view, based on several specimens. F. Pygidium, based on specimen in Pl. 102, figs. 1, 3, 4.

EXPLANATION OF PLATE 101

Figs. 1–17. *Lygdozoon collatum* n. sp., St. Clair Limestone (Wenlockian), Batesville district, Arkansas. 1, 3, 10. Holotype, incomplete cephalon USNM 256007; 1, 3, dorsal and right oblique views, × 1·7; 10, enlargement of anterolateral part of frontal glabellar lobe, showing large pit and granules on the exoskeleton, × 5·8. Locality USNM 438c. 2. Hypostome USNM 298947; ventral view, × 4·1. Locality H. 4, 9. Incomplete cephalon USNM 298949; lateral and ventral views, × 2·5. Locality USNM 286v. 5. Exfoliated hypostome USNM 298951; ventral view, × 3·9. Locality USNM 438c. 6, 12. Small cephalon USNM 256008; lateral and dorsal views, × 3·2. Locality USNM 286v. 7. Doublure of cephalon USNM 298948; ventral view, × 2·6. Locality H. 8, 11. Incomplete and exfoliated large cephalon USNM 256010; dorsal and lateral views, × 1·4. Locality H. 13, 15. Incomplete cephalon USNM 256011; anterior and dorsal views, × 1·6. Locality USNM 286v. 14. Cephalon USNM 298946; dorsal view, × 2·9. Locality USNM 438c. 16, 17. Pygidium USNM 298945; dorsal and lateral views, × 2·1. Locality USNM 438c.

PLATE 101



HOLLOWAY, *Lygdozoon*

Description. Cephalon subtriangular in outline, length (sag.) three-fifths the width at the posterior border. Posterior margin gently deflected backwards at the fulcrum and reflexed outwards (in large specimens distinctly forwards) distally. Genal spines diverge at the base and slightly converge distally, continuing the curvature of the lateral cephalic margin in dorsal and lateral profiles. Glabella subpentagonal in outline, equal in width at the occipital ring and 1p lobe and thereafter expanding anteriorly, bulging slightly at the 3p lobe. Maximum glabellar width twice the minimum width. Occipital ring well rounded sagittally and exsagittally, bearing a small tubercle medially and weak nodes distally (more distinct in smaller specimens); occipital furrow transverse medially, deflected backwards abaxially to apodemes that are almost equidimensional in cross section. Glabellar lobe 1p shorter (exsag.) than the outer part of the occipital ring; 3p as long adaxially as the 2p lobe, expanding to twice this length abaxially. Inner ends of glabellar furrows joined by a faint longitudinal furrow; 1p furrow parallel to the outer part of the occipital furrow; 2p furrow straight and oblique; 3p expanding abaxially and just failing to reach the axial furrow. Frontal lobe subrhombic, more than half the length (sag.) of the glabella. Axial furrow shallowest at the widest part of the 3p lobe, deepest at the front of the palpebral lobe, dying out at the maximum glabellar width. Preglabellar furrow not impressed but visible as a fine line in the surface sculpture (Pl. 101, figs. 3, 6).

At its midpoint the palpebral lobe is flattened and only slightly higher than the palpebral area; narrow rim on the palpebral lobe is defined by a row of discrete linear pits. Visual surface more steeply sloping posteriorly than anteriorly but not appreciably higher; typical lens formula is 2 5 6 7 8 9 9 9 8 9 9 8 9 8 9 9 9 9 9 9 9 9 9 8 8 9 8 7 8 7 6 6 5 3 2; a very small accessory lens present at the top of some files. Anterolaterally to the eye, the cheek is inclined at almost the same angle as the visual surface; this slope decreases posteriorly and the convexity of the cheek increases. Anterior branch of the facial suture parallel to the axial furrow from γ to β, thereafter running around the front of the glabella in a sharp groove; posterior branch initially follows the lower edge of the eye before curving across the cheek in a broad arc. A distinct postocular furrow runs close behind the posterior branch of the suture. Dorsal surface of lateral border steeply inclined; lateral border furrow well defined, except anteriorly and posteriorly. Posterior border tapers from the axial furrow to the fulcrum and bears a short (exsag.) articulating flange, thereafter it expands to 1·5 times its proximal length; posterior border furrow with steep walls and gently rounded base, deepest at the fulcrum. Anterior part of cephalic doublure crescentic, gently convex, with a faint furrow crossing the inner edge obliquely at the distal end of the hypostomal suture.

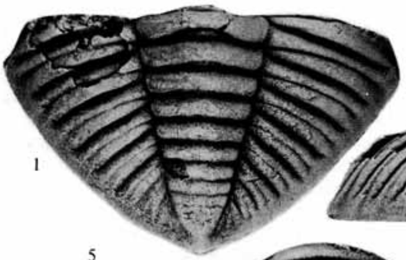
Granules coarser on dorsal surface of cephalon than on doublure, absent in furrows (except the lateral border furrow) and along the inside of the genal spine. Interspersed with granules on the cheek are irregularly shaped pits that extend into the lateral border furrow but not on to the border (Pl. 101, fig. 11). Fine pits (probably openings of cuticular perforations) occur along the front of the posterior border furrow, in the postocular furrow, and in the angle between the posterior branch of the suture and the eye. Large elliptical or lobate impression present on the anterolateral region of the frontal glabellar lobe (Pl. 101, fig. 10); similar but much smaller impressions form a transverse row above the preglabellar furrow. On internal moulds gentle swellings present on the front of the glabella.

EXPLANATION OF PLATE 102

All specimens from St. Clair Limestone (Wenlockian), Batesville district, Arkansas.

Figs. 1–13. *Lygdozoon collatum* n. sp. 1, 3, 4. Pygidium USNM 256012; dorsal, posterior and lateral views, × 2·0. Exact locality unknown. 2. Thoracic segment with rounded pleural tip USNM 298937; dorsolateral view, × 3·0. Locality H. 5, 7. Thoracic segment with orthogonal pleural tip USNM 298943; 5, dorsal view, × 1·9; 7, enlargement of pleura in dorsolateral view, × 3·7. Locality H. 6. Internal mould of pygidium USNM 298950; dorsal view, × 1·2. Locality USNM 438c. 8. Latex cast of external mould of doublure on thoracic segment with orthogonal pleural tip USNM 298938; ventrolateral view (front of segment at top of photograph), × 4·6. Locality H. 9. Latex cast of external mould of doublure on thoracic segment with rounded pleural tip USNM 298941; ventrolateral view (front of segment at top of photograph), × 3·1. Locality USNM 438c. 10, 11. Pygidium USNM 298940; ventral and lateral views, × 2·2. Locality USNM 286v. 12, 13. Incomplete and exfoliated thoracic segment with rounded pleural tip USNM 298942; 12, dorsal view, × 1·8; 13, enlargement of pleural tip in dorsolateral view, × 3·3. Locality H.

Figs. 14–21. *Lygdozoon anoplos* n. sp. 14–16. Holotype, incomplete cephalon USNM 298952; lateral, ventral and dorsal views, × 2·3. Locality O. 17. Incomplete pygidium USNM 298954; dorsal view, × 2·5. Locality O. 18, 21. Weathered cephalon PU 57685, paralectotype of *L. arkansanum* (Van Ingen); lateral and dorsal views, × 2·4. Locality USNM 286w. 19, 20. Pygidium USNM 298953; dorsal and lateral views, × 3·0. Locality O.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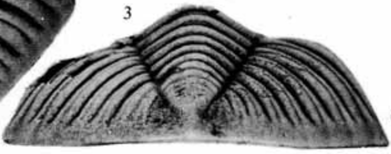
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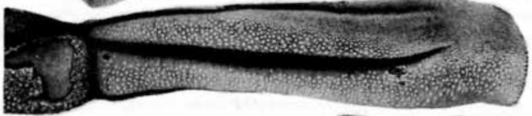
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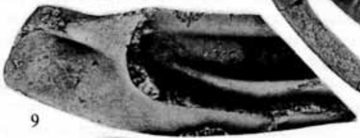
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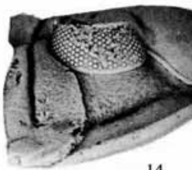
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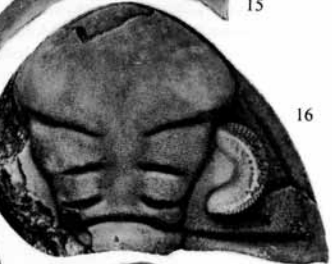
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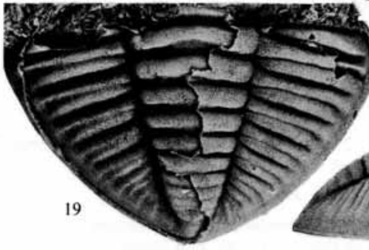
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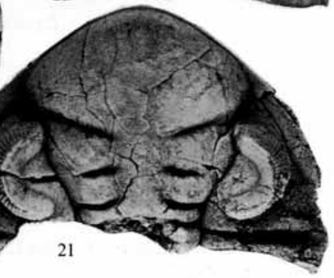
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HOLLOWAY, *Lygdozoon*

Hypostome 1·2 times as wide across the anterior wings as long (sag.); lateral margins converge gently between the anterior wing and the shoulder (situated behind the hypostomal midlength), more strongly behind the shoulder; median and two lateral denticles present on posterior margin. Lateral border narrow, strongly rounded (tr.), of almost constant width except posteriorly; posterior border subcrescentic, flattened (sag., exsag.). Lateral and posterior border furrows sharply impressed, with a distinct break in curvature at the shoulder. Middle body as long as wide, more convex transversely than sagittally; middle furrow weak except for a pronounced deepening at the macula. Outer surface of hypostome covered with very fine granules and indistinct swellings (more prominent on internal moulds); crater like pits on inner surface represented on internal moulds by fine pits with a central swelling.

Number of thoracic segments unknown. Axial ring turned slightly forwards abaxially and weakly expanded; articulating half ring more convex (sag., exsag., tr.) than the ring proper and about half as long; articulating furrow decreases in length (exsag.) abaxially and curves steeply downwards into the oblique apodemal pit. Axial furrow well defined across the whole segment and bowed outwards. Pleural furrow almost straight except where it is flexed forwards distally on to the articulating facet; anterior pleural band longer (exsag.) at the fulcrum than the posterior band. On round-tipped (more anterior) segments the rear edge of the pleura curves forwards distally; on truncated-tipped (more posterior) segments it curves outwards abaxially and then is deflected slightly backwards distally. Short (exsag.) articulating flanges present along the anterior and posterior edges of the pleurae; posterior flange dies out at the fulcrum; small process present at the proximal end of the anterior flange (Pl. 102, fig. 7). Anterior articulating furrow extends partly across the facet, though much reduced in strength, and separates a flat, abaxially expanding band. On segments with truncated pleural tips the front of the facet is cut away beyond this band, the distal end of which forms a blunt process (Pl. 102, fig. 7); on round-tipped segments there is instead a small protuberance on the front of the facet (Pl. 102, fig. 13). Doublure beneath the pleural tips broad (tr.), with a well-developed panderian protuberance against which the anterior edge of the succeeding segment abutted on enrollment (Pl. 102, figs. 8, 9). Inner edge of doublure more arcuate in round-tipped segments than in the other type, meeting the anterior edge of the segment at the process on the front of the facet.

Pygidium subtriangular, maximum width (level with the second ring furrow) approximately 1·5 times the length. Axis tapers uniformly backwards, except posteriorly; axial furrow firmly impressed but transgressed by the ring and interpleural furrows. Anterior axial rings with maximum curvature (tr.) medially, posterior ones evenly arched (Pl. 102, fig. 3); first ring inclined forwards with respect to the rest, tapering medially to three-quarters its distal length (exsag.); subsequent rings of uniform length (sag., exsag.) across the axis. Pseudo-articulating half rings present on the second and third axial rings, that on the third being tiny and poorly differentiated. Ring furrows shallow medially, first six with apodemal pits abaxially (Pl. 102, fig. 6). Pleurae gently convex, postaxial region steeply inclined. Pleural furrows similar to those on thorax except that the first does not curve forwards distally on to the articulating facet. Interpleural furrows gently arcuate, thin and sharp, deepening slightly proximally and distally. Pleural and interpleural furrows terminate abruptly just inside the margin, but faint extensions of the interpleural furrows reach the margin. Doublure narrow, outer part gently rounded, inner flange turned strongly upwards and slightly outwards.

Coarse granules present on the axial rings and pleural bands of thorax and pygidium, across the back of the articulating and pseudo-articulating half rings, and extending down the anterior slope of the thoracic pleural furrows. Anterior bands of the articulating facets smooth, but the remainder of the facets covered with tiny granules (Pl. 102, figs. 7, 13). Doublure on the thoracic segments mostly smooth but weak granules present in front of the panderian protuberance (Pl. 102, fig. 8). Fine granules on the pygidial doublure do not extend on to the inner flange.

Lygdozoon arkansanum (Van Ingen, 1901)

Plate 98, fig. 14; Plate 103, figs. 9, 12, 14–16, 18, 19; text-fig. 3.

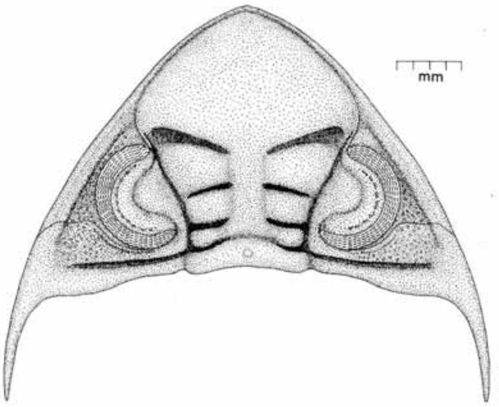
v* 1901 *Dalmanites* (*Synphoria*) *arkansanus* Van Ingen; Van Ingen, pp. 69–73 (in part), text-figs 20, 22 (not text-fig. 21 = *Lygdozoon* sp. 1 herein).
v. *non* 1907 *Dalmanites arkansanus* Van Ingen; Weller, pp. 278–280, pl. 24, fig. 5.
. *non* 1929 *Dalmanites arkansana* Van Ingen; Thomas, pp. 125–126, pl. 10, figs. 12–14 (= *L. collatum*).
v. 1940 *Dalmanitina arkansana* (Van Ingen); Delo, p. 54, pl. 4, figs. 1, 2.
v. *non* 1954 *Dalmanitina arkansana* (Van Ingen); Allen and Lester, p. 71, pl. 19, fig. 3.

Type material. All from the St. Clair Limestone, Locality USNM 286w, Batesville district, Arkansas. Lectotype (here designated): PU 49534 (Pl. 103, figs. 15, 16, 19), incomplete cephalon figured by Van Ingen (1901, text-fig.

20) and Delo (1940, pl. 4, fig. 1; note that right and left are reversed in this photograph). Paralectotypes: PU 57684 (Pl. 103, figs. 9, 12), incomplete cephalon; PU 49536 (Pl. 103, fig. 18), almost complete pygidium figured by Van Ingen (1901, text-fig. 22) and Delo (1940, pl. 4, fig. 2); PU 57676, 57678, 57680, 57738 (Pl. 98, fig. 14), small and incomplete cephala. Several additional cephala and pygidia included in *Dalmanites* (*Synphoria*) *arkansanus* by Van Ingen are here referred to either *L. anoplos* or to *Lygdozoon* sp. 1.

Other material. A small cephalon PU 88120, from Locality USNM 286w.

Diagnosis. Cephalon markedly subtriangular in outline, genal spines present. Glabella expanding strongly forwards, bulging weakly at 3p lobe; lateral glabellar lobes slightly inflated, separated from median part of glabella by shallow longitudinal furrows; frontal glabellar lobe depressed. Eye very large, extending backwards and inwards almost to axial and posterior border furrows, in plan view forming an arc subtending an angle of about 240°, containing thirty-three dorsoventral lens files with up to nine lenses each. Cephalic doublure long (sag.) medially, subtriangular. Pygidium with ten axial rings and pleural furrows. Surface of cephalon and pygidium densely covered with granules of uniform size.



TEXT-FIG. 3. Reconstruction of cephalon of *Lygdozoon arkansanum* (Van Ingen, 1901) based on specimen in Pl. 103, figs. 15, 16, 19.

Remarks. L. arkansanum is distinguished from *L. collatum* by the following features.

1. The cephalic outline is straighter along the sides and rather more pointed medially.
2. The lateral glabellar lobes are more inflated, particularly 3p, and are more distinctly separated from the median part of the glabella by longitudinal furrows. The 3p lobes do not bulge as stongly abaxially and the 3p furrows are deeper. The frontal glabellar lobe is more depressed (compare Pl. 101, fig. 4 and Pl. 103, fig. 15).
3. In at least the lectotype, the 3p furrows are not as oblique, so that the frontal glabellar lobe is almost subtriangular in outline rather than rhombic. Other specimens of *L. arkansanum* suggest that the shape of the frontal glabellar lobe is not constant within the species but the amount of variation cannot be determined from the limited material available.
4. The eyes are relatively larger and more arcuate in plan.
5. After diverging from the lower edge of the eye, the posterior branch of the facial suture (at least in large holaspids) does not run across the cheek in a curve but turns sharply outwards and crosses the lateral border furrow with a gentle backward deflection.
6. The medial part of the doublure is relatively longer and subtriangular in shape rather than crescentic (compare Pl. 101, figs. 7, 9 and Pl. 103, fig. 9).

Amongst the specimens referred to this species by Van Ingen, there is only one pygidium with a surface sculpture similar to that of the lectotype and it seems to be indistinguishable from pygidia of *L. collatum* (Pl. 103, fig. 18).

Several of the cephala belong to small holaspids of *L. arkansanum* and in these the cephalic outline is more arcuate along the sides than it is in larger specimens; the apodemes are equally spaced; the 1p furrow tends to bifurcate proximally; the occipital ring has distinct lateral nodes and a large median tubercle; the posterior branch of the facial suture is convex forwards; and (in very small cephala) the exoskeleton is covered with granules of two sizes instead of uniform granules (Pl. 98, fig. 14).

Examination of the cephalic mould from the Niagaran of Romeo, Illinois described and figured by Weller (1907, pl. 24, fig. 5) as *Dalmanites arkansanus* shows that it differs from the present species in that the anterior glabellar outline is not as flattened along the sides and is not as pointed medially; the frontal glabellar lobe is relatively shorter (sag.), is not as depressed, and falls abruptly to the anterior border furrow; the eyes are not as arcuate in plan and do not extend as close to the axial furrow posteriorly; and the posterior branch of the facial suture curves in an arc across the cheek. Allen and Lester (1954) reported the present species under the name *Dalmanitina arkansana* from the Llandoverian Red Mountain Formation of Georgia. Their specimens, which are now in the U.S. National Museum of History, consist of a cranidium possibly belonging to *Stenopareia* and a pygidium belonging to a calymenid.

Lygdozoon anoplos n. sp.

Plate 102, figs. 14–21; text-fig. 4A

v. 1901 *Dalmanites* (*Synphoria*) *arkansanus* Van Ingen; Van Ingen, pp. 69–74 (in part).

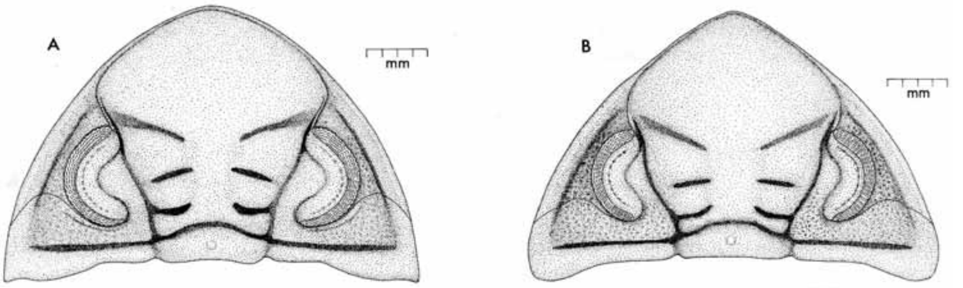
Name. Greek 'anoplos' meaning unarmed, referring to the lack of genal spines.

Type material. All from the St. Clair Limestone, Locality O, Batesville district, Arkansas. Holotype: USNM 298952, incomplete cephalon; Pl. 102, figs. 14–16. Paratypes: USNM 298953-4, pygidia.

Other material. Incomplete cephalon PU 57685, a paralectotype of *Dalmanites* (*Synphoria*) *arkansanus*, from the St. Clair Limestone at Locality USNM 286w.

Diagnosis. Genal angle pointed, spine lacking. Glabella rather flattened (tr.) across lateral lobes. Pygidium with about nine axial rings and eight, rather thin pleural furrows, last two of each weakly defined. Surface granulate, more finely on pygidium than on cephalon.

Remarks. The exact arrangement of lenses in the eye of the holotype is indeterminate but there are about thirty-three dorsoventral files with a maximum of at least nine lenses each. Apart from the lack of genal spines, the cephalon of *L. anoplos* differs from that of *L. collatum* in having a glabella that is more flattened (tr.) across the lateral lobes; eyes that are less arcuate in plan and do not extend as close to the sagittal axis posteriorly; more sparsely tuberculate lateral glabellar lobes; and no granules on the lateral border. The pygidia have relatively thinner pleural furrows that are not directed as



TEXT-FIG. 4. A. Reconstruction of cephalon of *Lygdozoon anoplos* n. sp., based on specimen in Pl. 102, figs. 14–16. B. Reconstruction of cephalon of *Lygdozoon* sp. 2, based on specimen in Pl. 103, figs. 5, 8, 11.

strongly backwards; flatter (sag., exsag.) axial rings; one or two fewer axial rings and pleural furrows; and finer exoskeletal granulation.

The cephalon PU 57685 (Pl. 102, figs. 18, 21) differs from the holotype in that the glabella is not as flattened across the lateral lobes, and the eye is relatively lower, having only thirty-one dorsoventral lens files each with a maximum of seven lenses. The genal angles are broken, so that it is not definitely known whether genal spines were present, although what remains of the posterior border on the left side suggests that they were not. The dorsal surface sculpture has been entirely obliterated by weathering.

Lygdozoon sp. 1

Plate 103, figs. 1–3, 7, 10, 13

v. 1901 *Dalmanites* (*Synphoria*) *arkansanus* Van Ingen; Van Ingen, pp. 69–74 (in part), text-fig. 21 (not text-figs. 20, 22).

Material. From the St. Clair Limestone at Locality USNM 286w, Batesville district, Arkansas: PU 49535, incomplete cephalon figured by Van Ingen (1901, text-fig. 21); PU 57635, incomplete cephalon; and possibly PU 57681-2, two small pygidia.

Remarks. The two cephala included in this species were considered by Van Ingen (1901) to belong to the 'female' of *Dalmanites* (*Synphoria*) *arkansanus*. They are characterized by well-rounded genal angles; glabellar furrows 1p that distinctly curve forwards proximally as well as distally; glabellar furrows 2p that are transverse instead of slightly oblique; and eyes that are equidistant from the sagittal axis anteriorly and posteriorly, and are composed of a very large number of small lenses. The right eye of PU 49535 has thirty-six dorsoventral lens files. The upper part of the eye is broken off but near the middle (exsag.) of the eye there are up to eight lenses remaining in each file; I estimate that there must originally have been 12 to 14 lenses in the longest dorsoventral file. The same specimen has a sculpture of granules of two sizes on the glabella and the inner part of the cheek. The surface of the glabella in the other cephalon appears to have been abraded and the sculpture is poorly preserved.

Two fairly small pygidia amongst Van Ingen's specimens are thought possibly to belong to the same species as the cephala described above, because one of them has a sculpture of bimodal granules. The surface sculpture is not preserved on the other pygidium. Alternatively, these pygidia may belong to juveniles of *L. arkansanum* since small cephala of that species also have granules of two sizes on the exoskeleton. However they are sufficiently different to the paralectotype pygidium of *L. arkansanum* to suggest that this is unlikely. The pygidia have eleven axial rings and nine pleural furrows, with evidence of two more pleural segments behind that. The pleural furrows are thinner and not directed as strongly backwards as in *L. arkansanum*, while the interpleural furrows extend distinctly to the outer margin, which is weakly scalloped on the first few segments.

Lygdozoon sp. 2

Plate 103, figs. 4, 5, 6, 8, 11, 17; text-fig. 4B

Material. From the St. Clair Limestone at Locality B, Batesville district, Arkansas: two incomplete cephala, USNM 298956-7, and an incomplete pygidium, USNM 298955.

Remarks. The cephalon has rounded genal angles and the anterior outline is rather pointed medially. The eye is situated almost as far from the sagittal axis posteriorly as anteriorly and is not strongly curved in plan. It contains about twenty-nine dorsoventral lens files of up to eleven lenses each. The other species of *Lygdozoon* described here have flat palpebral lobes but in this species the palpebral lobe rises fairly steeply from the palpebral furrow and turns outwards along the crest, which is slightly higher than the outer palpebral rim. The frontal glabellar lobe is covered with small granules but the remainder of the glabella is almost completely smooth, apart from a cluster of granules around the median occipital tubercle, and very coarse granules lining the glabellar and outer part of the occipital furrows. Similar granules line the posterior border furrow but the crests of the posterior and lateral borders are smooth. On the cheek below the eye are very coarse granules with interspersed pits; the pits but not the granules extend inwards behind the eye to the axial furrow. There are small granules on the crest of the palpebral lobe but the inwardly sloping portion is smooth. The cephalon of *Lygdozoon* sp. 2 is very similar to that of *Lygdozoon* sp. 1 but is distinguished by the surface sculpture, the smaller number of lenses in the eye, and the inclined palpebral lobe.

The pygidium of *Lygdozoon* sp. 2 has ten axial rings and nine pleural furrows, the first six pleural furrows being very deeply incised. There are successively diminishing pseudo-articulating half rings on segments 2 to 6 and beyond that they become indistinguishable. Just inside the outer pleural margin is a gentle groove defining a very thin rim. There are rows of prominent granules along the back of the anterior pleural bands and the axial rings (more of a cluster of granules on the medial part of the latter), and the articulating facets are finely granulate. Apart from this the surface of the pygidium is completely smooth.

ORIGINS OF THE DALMANITINAE AND SYNPHORIINAE

The majority of Silurian dalmanitinids are presently referred to the genus *Dalmanites*, the earliest representatives of which appear to be of Wenlockian age. However, several forms in which the diagnostic characters of the subfamily are not fully developed are found in Late Llandoverian strata, and these include *Daytonia*, *Prodontochile* Kobayashi and Hamada, 1971, and the species '*Phacops*' *weaveri* Salter, 1864; the last two have been commented on in the remarks on *Daytonia*. The Dalmanitinae almost certainly arose from a member of the Mucronaspidinae, and it is my view that *Daytonia* is phylogenetically intermediate between these subfamilies. The most likely ancestor of *Daytonia* is *Eudolatites*, these genera being very close in the shape of the glabella and the form of the glabellar furrows; the width and convexity of the lateral cephalic borders; the form of the posterior and lateral cephalic border furrows; the shapes of the thoracic pleural tips and the termination of the thoracic pleural furrows; and the over-all form of the pygidium, including the number of segments, the curvature of the pleural and interpleural furrows, the well-defined border, and the distinct terminus on the axis. Struve (1958, p. 210; *in* Moore, 1959, p. O475) noted the similarity between *Eudolatites* and members of the Dalmanitinae. Transformations necessary to produce the morphology of *Daytonia* from *Eudolatites* include the increase in length of the anterior cephalic border and development of a slight anterior process; development of a 2p apodeme; enlargement of the eyes; formation of blade-like genal spines; and expansion (exsag.) of the pleural furrows on the thorax and pygidium. All later dalmanitinids could have been produced from the morphology of *Daytonia*

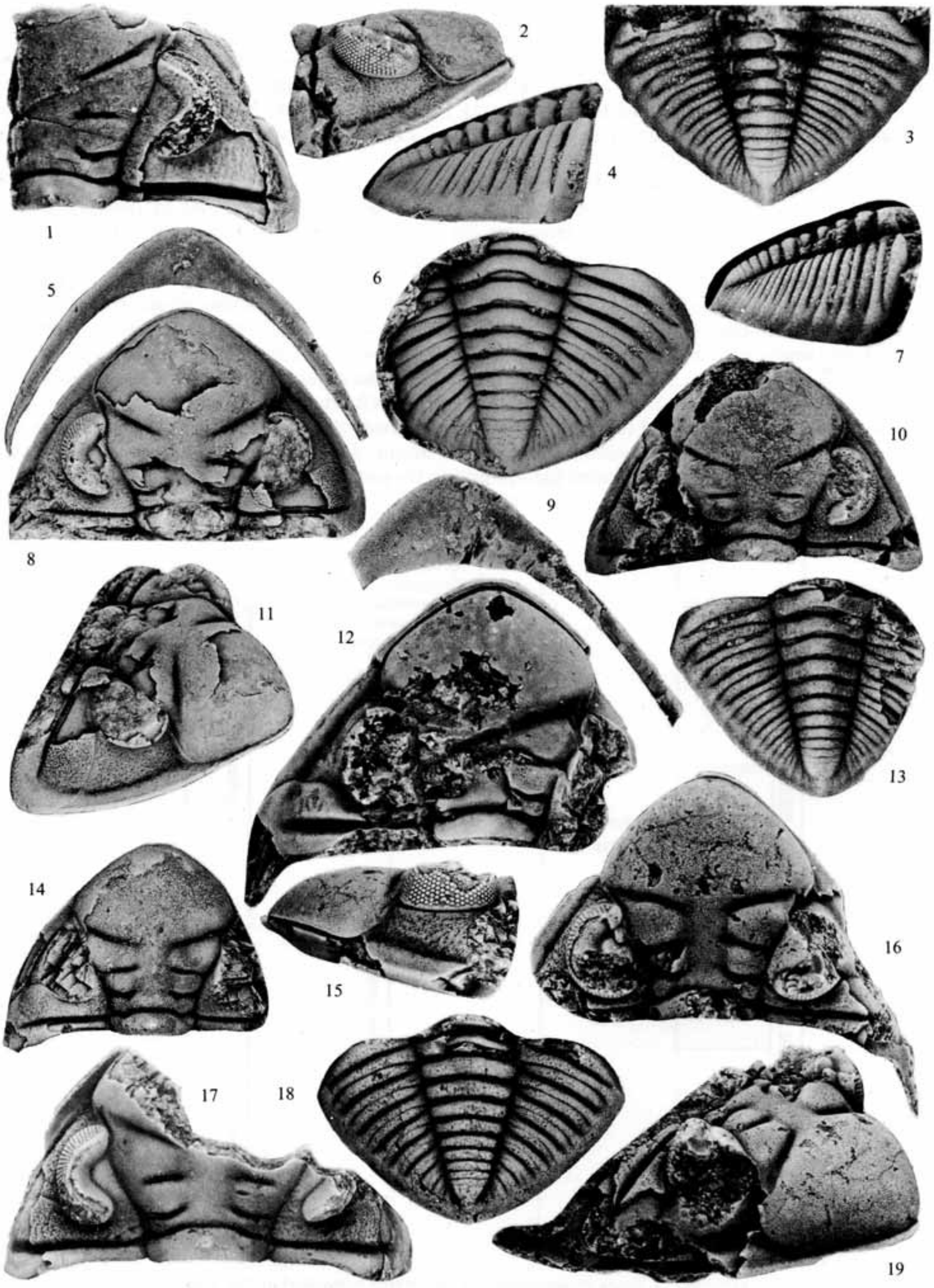
EXPLANATION OF PLATE 103

All specimens from St. Clair Limestone (Wenlockian), Batesville district, Arkansas.

Figs. 1–3, 7, 10, 13. *Lygdozoon* sp. 1. Locality USNM 286w. 1. Incomplete cephalon PU 57635, paralectotype of *L. arkansanum* (Van Ingen); dorsal view, × 2·4. 2, 10. Cephalon PU 49535, paralectotype of *L. arkansanum* (Van Ingen), figured by Van Ingen (1901, text-fig. 21); lateral and dorsal views, × 2·5. 3, 7. Small pygidium PU 57682, paralectotype of *L. arkansanum* (Van Ingen); dorsal and lateral views, × 7·1. 13. Small, incomplete pygidium PU 57681, paralectotype of *L. arkansanum* (Van Ingen); dorsal view, × 5·1.

Figs. 4–6, 8, 11, 17. *Lygdozoon* sp. 2. Locality B. 4, 6. Latex cast of external mould of pygidium USNM 298955; lateral and dorsal views, × 3·4. 5, 8, 11. Cephalon USNM 298956; ventral, dorsal and right oblique views, × 2·3. 17. Incomplete cephalon USNM 298957; dorsal view, × 2·1.

Figs. 9, 12, 14–16, 18, 19. *Lygdozoon arkansanum* (Van Ingen, 1901). Locality USNM 286w. 9, 12. Paralectotype, cephalon with exfoliated dorsal surface PU 57684; ventral and dorsal views, × 2·2. 14. Small cephalon PU 88120; dorsal view, × 3·1. 15, 16, 19. Lectotype, cephalon PU 49534, figured by Van Ingen (1901, text-fig. 20) and Delo (1940, pl. 4, fig. 1); lateral, dorsal and right oblique views, × 2·2. 18. Paralectotype, pygidium PU 49536, figured by Van Ingen (1901, text-fig. 22) and Delo (1940, pl. 4, fig. 2); dorsal view, × 3·0.

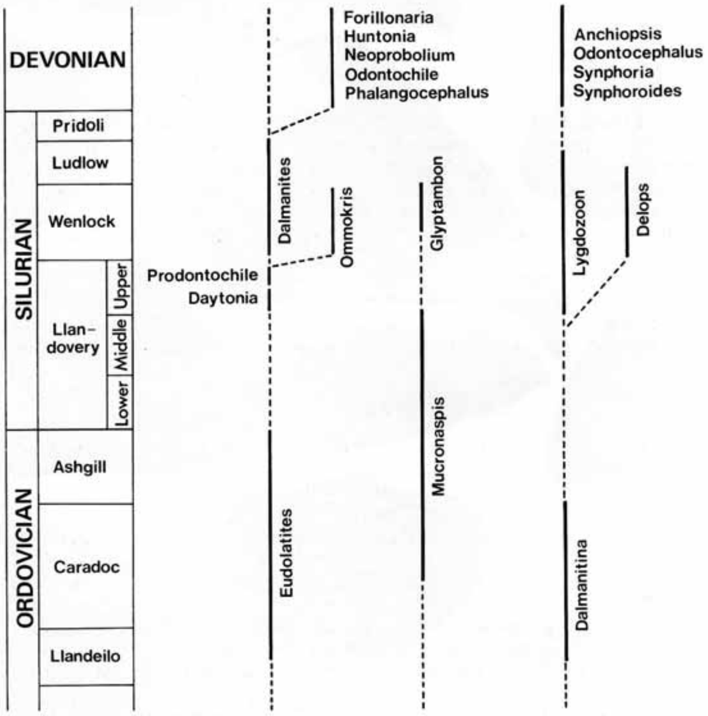


HOLLOWAY, *Lygdozoon*

by modification of the glabellar furrows; increase in the width and degree of flattening of the lateral cephalic border, and development of an epiborder furrow; enlargement of the genal spines; formation of lanceolate posterior cephalic border furrows and thoracic pleural furrows; deflection of the thoracic pleural furrows behind the articulating facets distally; and weakening of the posterior pleural bands on the pygidium. The age of *Daytonia* suggests that the Dalmanitinae arose during Middle-Late Llandovery time.

The ancestry of the genus *Glyptambon* probably also lies in the Mucronaspidinae, which it resembles in the form of the thoracic pleural tips and pleural furrows, and in the pleural and interpleural furrows on the pygidium. However, the fact that the pygidial axis merges with the mucro instead of having a distinct terminus suggests that *Glyptambon* was derived from a form such as *Mucronaspis* rather than from *Eudolatites*.

The morphology of the Synphoriinae is consistent with the subfamily having arisen from a member of the Dalmanitininae, and possibly from *Dalmanitina* itself or one of its descendants. There are remarkable similarities between *Dalmanitina* and *Lygdozoon* in the form of the cephalic borders and doublure; the genal spines; the shape of the middle body of the hypostome and the form of the middle furrow and the maculae; the thoracic architecture, including the pleural furrows and their relationships to the facets, and the well-rounded pleural bands; the form of the pygidial pleural and interpleural furrows; and the pygidial doublure. An origin of the Synphoriinae in *Dalmanitina* also offers an explanation for the truncated pleural tips on the posterior thoracic segments of *Lygdozoon*.



TEXT-FIG. 5. Some evolutionary relationships suggested in this paper.

Of course the pleural tips on the more anterior thoracic segments of *Lygdozoon* are not exactly like those of *Dalmanitina*, but it is possible to envisage how they might have been produced from the *Dalmanitina* pattern by enlargement of the process on the posterior edge of the pleural tip, rounding of the point of the process, and weakening of the notch in front of the process (see Pl. 100, figs. 8, 9). The anterior thoracic segments in *Lygdozoon* still retain a trace of a notch on the distal edge (Pl. 102, figs. 2, 13). Other features in which *Lygdozoon* seems to be closer to *Dalmanitina* than to Devonian synphoriinids include the more or less transverse 1p furrow, the relatively thick anterior pleural bands on the thorax, and the depth of the interpleural furrows on the pygidium. Further weight is added to the preceding argument by the striking resemblance between small holaspid cephala of *Lygdozoon* and *Dalmanitina* cephala (Pl. 98, fig. 14; Pl. 103, fig. 14).

Two objections can be made against the proposal that the Synphoriinae evolved from the Dalmanitininae. The first concerns the time difference between the occurrence of *Lygdozoon* and the latest known species of *Dalmanitina*, which are of late Caradoc or possibly Ashgill age. The second objection involves biogeography, since *Lygdozoon* and post Devonian synphoriinids seem to be exclusively North American in distribution, whereas there is no record of dalmanitininids in the Ordovician of North America, though they are abundant in Europe. However *Delops*, which was presumably derived from the same stock as *Lygdozoon*,,occurs in both Europe and North America. It is possible that *Lygdozoon* and *Delops* both originated in Europe. At any rate, I believe that the arguments based on the morphology of *Lygdozoon* and *Dalmanitina* outweigh these objections.

Lespérance (1975) and Campbell (1977) were of the opinion that the Trypaulitinae arose from the same stock as the Synphoriinae. However, *Lygdozoon* has no features that are reminiscent of the Trypaulitinae, and furthermore I can see no way in which it could have given rise to a trypaulitinid morphology, particularly with regard to the differences in the cephalic borders, the genal spines, and the form of the thoracic pleural tips. If the trypaulitinids and the synphoriinids do have a common origin, they must have separated considerably before the Wenlockian.

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